JOHN MARION THODAY
30 August 1916 — 25 August 2008
Professor John M. Thoday, ScD, FRS, was Arthur Balfour Professor of Genetics at the University of Cambridge from 1959 until 1983. In that position, he was influential in establishing genetics as an integral part of the undergraduate programme in biology at Cambridge, and he developed an active research programme that explored genetic processes underlying quantitative genetic traits, natural selection in sympatric populations and genetic variation in human and other populations. In more than 125 publications, he brought insightful attention to questions that had often been overlooked by others. Some of his most significant work explored the genetic basis of quantitative traits and thus pioneered approaches to understanding the mechanisms behind responses to selection. This helped set the stage to uncovering genes in the multiple-gene systems that determine polygenic characters in fields from medicine to agriculture. Other key work focused on disruptive, or diversifying, selection as a potential mechanism for populations to respond to adaptive challenges in nature. When his study of disruptive selection began, many in the field believed it was not even a possible process. In his many roles, John Thoday was a mentor who stimulated an open, respectful and intellectually rich academic environment for the Department of Genetics at Cambridge and for his field of creative activity.

EARLY LIFE AND SCIENTIFIC INFLUENCES

John Thoday was born in Chinley, Derbyshire, in 1916, the third son of Professor David Thoday (FRS 1942) and Mary Gladys Thoday. David Thoday was at that time a lecturer in
botany at the University of Manchester. After a short spell in Cape Town, South Africa, David Thoday then moved back to the UK to become a professor in Bangor in 1922, allegedly at the instigation of the then professor of botany at Cambridge, who had a major influence on academic appointments. John Thoday’s mother, Mary, also a botanist, was a strong character who campaigned actively both for women’s rights and for the Women’s Peace Movement, activities that David Thoday condoned without actively approving. Coming from a family where both parents were botanists, John Thoday recalls that as an 11- or 12-year-old child he went on botanical excursions with undergraduates during the vacations.

He went to a number of different schools, ending up in Bootham School, York, a Quaker independent school, where he credited an inspiring physics teacher for awakening his interest in science and the scientific method.

From school he went on to read science at Bangor in 1934, and he had some scathing remembrances of the rote learning that was a feature of much of the science teaching of the time. His impatient intellect did not see why one had to learn every phase of embryonic development before you could ask questions about why development should happen in a particular way.

However, in 1938, while in his honours year, he attended a John Innes summer school in London and was excited to hear C. D. Darlington (FRS 1941) talk about chromosomes and T. J. C. Lawrence talk about the genetics of anthocyanin pigmentation. The John Innes Horticultural Institution was at the time doing pioneering work on the enzymes involved in flower pigment formation. He was greatly taken by the empirical and experimental approach to such problems, and, following graduation from Bangor, began his PhD studies in the Botany School in Cambridge under the supervision of D. G. Catcheside (FRS 1951).

The subject of his research was the effect of radiation (X-rays and neutrons) on chromosomes, using pollen grain mitosis in *Tradescantia bracteata* as his experimental material.

He was able to show that chromosome damage was roughly dependent on radiation dose, but his research was soon interrupted by military service in the RAF. Thoday volunteered for military service in 1940 and was given the choice of radar or photographic intelligence work. He chose the latter, perhaps because the fossil botanist in the Cambridge Botany School, H. Hamshaw Thomas FRS, had been involved in photo intelligence in World War I and was then actively recruiting for the RAF. The RAF sent him to the Middle East as a liaison officer in photographic intelligence, where at one stage his immediate superior was Enoch Powell. During his war service he moved from Cairo to Algiers and eventually to Italy following the Allied landings there.

He was later to describe his five years of war service as ‘wilderness years’ in the sense that he was too busy and too far from any sources of information to have any contact with science. He had read Darlington’s *Evolution of genetic systems* (Darlington 1939) before entering the RAF, and this proved to be something of a seminal influence on his thinking about the problem of genetic fitness. Some of his ideas about components of fitness (4)* date from this period of scientific exile. In later years he relished recounting his experiences of the desert—the heat, the dust, the flies, the chaos and confusion of the conflict—but he also had fond memories of the camaraderie and the sense of purpose that came to many of his generation who served in World War II.

* Numbers in this form refer to the bibliography at the end of the text.
Discharged with a commission in 1945, Thoday resumed his academic studies, and his first job in 1946 was as a cytologist at Mount Vernon Hospital in London. This was just after the use of the atomic bomb on Hiroshima and Nagasaki. Radiotherapy was beginning to be used for cancer treatment, and there was a realization that science urgently needed to know more about the effects of different kinds of radiation on biological tissue. The view at the time was that radiation interacted directly with chromosomes, and the predictions from radiation physics were that alpha particles should be less effective at causing damage than X-rays. In fact alpha particles did cause chromosome damage, and Thoday was able to show that the presence of oxygen increased the ability of both alpha particles and X-rays to break and damage chromosomes, probably owing to the formation of peroxides and free radicals (1–3). This was a significant discovery that was later to lead to a much better understanding of the role of radiation in inducing mutation and genetic variation. This work was a more or less direct continuation of the PhD research he had begun with Catcheside and Lea at Cambridge before the war. Although his findings were significant for radiation biology, Thoday was now becoming more interested in the genetic variation that occurred as a result of radiation damage than in an investigation of the damage process itself.

**ACADEMIC CAREER**

Thoday was offered a post as a cytobiologist at the University of Sheffield and moved there in October 1947 as an assistant lecturer, in a post that, unusually for the time, was assigned to both botany and zoology departments.

At this point, Thoday began experiments on selection using *Drosophila*. K. J. Mather (FRS 1949) had developed inbred lines of *Drosophila* and Thoday obtained these lines from Mather and interbred them to generate heterozygotes. These allowed him to investigate the interaction between genetic and phenotypic variation using sternopleural bristle numbers. This was a character that was genetically determined and also showed a continuous distribution of phenotype.

Work in Sheffield sparked an interest in teaching, and he helped the professor of botany, A. R. Clapham (FRS 1959), with first-year botany practicals. Dismissive of a rote learning approach, Thoday reorganized the practicals in such a way that students had to draw their own conclusions from the experimental material presented. Asked to teach a course on economic botany, he took the opportunity to turn it into a course on plant breeding.

By this time, Thoday’s work on selection was attracting interest and attention from the academic community, and he was beginning to build a scientific reputation. He received an invitation from Darlington to move to a position in Oxford, but his views on selection processes were beginning to differ from those of Darlington, and Thoday felt that it was easier to disagree with Darlington from a distance rather than from a position of close proximity. In 1954 Sheffield then promoted him to senior lecturer and created a department of genetics for him—without, however, giving him any more space or facilities.

His next move was to Cambridge, and it came about by a somewhat unusual route. On the retirement of R. A. Fisher’s FRS from the Cambridge chair of genetics, the electors had failed to agree on a candidate who was prepared to take it. G. Pontecorvo FRS and E. B. Ford FRS had both turned down offers, largely because the department had few facilities. It was located in what had been a large private house (Whittinghame Lodge), which had no proper...
laboratory space, and it had no established teaching profile in the university. For many years previously the only teaching of genetics for first and second year students had been a set of optional afternoon lectures, and unsurprisingly these had not been widely popular. There was a third year course in genetics, but, following Fisher’s interests, it was heavily mathematical and attracted only a few committed students.

The electors also failed to renew their term, so responsibility for the appointment reverted to the vice chancellor. The vice chancellor took advice, reputedly from Mather, and offered Thoday the chair, which he accepted. The University of Cambridge was perhaps conscious of the fact that, although W. Bateson, E. R. Saunders and R. C. Punnett (FRS 1912) had been instrumental between 1905 and 1910 in establishing genetics as fundamental to an understanding of biology, the Cambridge genetics department had not grown with the understanding of the subject through subsequent years. Thoday was offered another building, recently vacated by the Veterinary School, but located on the outskirts of town, and several new academic positions. He moved to Cambridge in 1959 and began the task of building up the presence of genetics in the university (figure 1).

His early years in Cambridge were devoted to the twin tasks of establishing the research and teaching profiles of the department. John Thoday always resisted being labelled as a particular brand of geneticist, and if pressed he would say that his real interest lay in the global questions of developmental biology and how a study of genetic variation could be used to help answer some of these questions. To that end he built up the Cambridge Department of Genetics by recruiting staff across the range of the subject, from microbial and plant genetics to the genetics of populations and evolutionary biology. During these early years W. F. Bodmer (FRS 1974) and L. Cavalli-Sforza (ForMemRS 1992) were both members of the department.
The department was still relatively small, and its location on the outskirts of Cambridge meant that it was still somewhat isolated from the rest of the biology departments. However, this did have the benefit that all staff and students met in the tea room or in the local pub for lunch, and both locations became an active forum for discussion and exchange of ideas.

The department was a comfortable place for a student to learn, test ideas, make mistakes and grow. Ideas were valued and shared widely. Group discussions at regular coffee and tea times focused on the strength of ideas, instead of being some arena of competition. Colleagues within the department were resources of information and of honest challenge. Thoday actively cultured this intellectual environment. He liked to challenge his colleagues and students, delighted in making provocative remarks to stimulate a thorough-going argument and had a fund of stories, some remarkably scurrilous, about the public and private lives of some of the major figures in twentieth-century genetics.

It was part of Thoday’s character to challenge existing dogma or, indeed, any views, scientific or otherwise, that he thought were built on questionable assumptions. This led to lively interchanges. Unlike many other Cambridge professors, some of whom were so aloof as to be invisible, he walked the shop floor regularly, appearing in laboratories to talk to staff and students about the work they were doing.

The early years in Cambridge were busy with research and building the department, and, as a result, Thoday did not spend a great deal of his time on grant awarding bodies or editorial boards. He maintained his personal research output with a small and highly focused team of researchers, with whom he could interact on a daily basis.

He did, however, chair an Organisation for Economic Cooperation and Development study group on biological education (20). As chair, Thoday had the difficult task of reconciling these views, and he recalls spending most of three nights drafting the eventual report. The meeting established the concept of teaching biology as an integrated and experimental science, which, although now the norm, was then something of a novel idea (21).

In addition to building the staff of the department, his other concern was to get genetics teaching embedded as an integral part of biology teaching, which meant getting genetics taught in first- and second-year courses. There were people in Cambridge who wished to integrate the teaching of biology, breaking down the traditional separation into subjects such as zoology and botany, and incorporating subjects like biochemistry and genetics. As with all such changes, there were battles to be fought against entrenched views. As chair of the Faculty Board of Biology, the body responsible for teaching, Thoday became heavily involved in these discussions, and he used his diplomatic skills to make a persuasive case for both the integration of biology teaching and the inclusion of genetics into the biology programme. Despite opposition from some of his academic colleagues to his championship of what to them was a new and upstart scientific discipline, he was eventually successful at this.

The final outcome of the discussions was the creation in 1965 of two interdepartmental first-year courses. One covered cellular biology and the other organismal and evolutionary biology, both involving a substantial component of genetics teaching. This was followed a few years later by other courses that incorporated genetics into second-year studies, and this greater exposure to the subject led to an increase in the number and quality of students reading genetics in their third year.

Thoday’s generalist approach to research was mirrored in his approach to the teaching of genetics. He felt strongly that students coming out of his department should have a basic
understanding of the range of genetics from molecular biology to evolutionary theory, and the final year teaching in genetics should reflect that philosophy.

As the research and teaching activities of the department expanded, its location on the fringe of town became a problem, and by 1977 Thoday had managed to persuade the university to move the department into larger premises on the university’s central Downing Site alongside most of the other biology departments.

By the time he retired in 1983, Thoday had the satisfaction of presiding over a thriving research department, which was also a core contributor to the teaching of biology in Cambridge. In addition to putting the Department of Genetics into the mainstream of biology research and teaching, he had played a significant part both in university administration, chairing major university committees involved with resource allocation, and as a fellow of Emmanuel College, where he is remembered as a keen bowls player.

**RESEARCH**

Beginning with his doctoral research on the effect of neutrons on chromosomes, which he completed at Trinity College, Cambridge, in 1939, Thoday’s choice of research questions paralleled his general curiosity about problems of broad applicability. Mention has already been made of his early, and significant, work on the role of oxygen in the increase of chromosome damage produced by radiation. As noted at a memorial service at Emmanuel College, Cambridge (Thompson 2008), Thoday enjoyed exploring phenomena that others dismissed or overlooked. He found novel insights that way. A prime example is his analysis of genes that contribute to continuous, or quantitative, variation in complex traits, using the fruit fly *Drosophila melanogaster* as the model organism.

When he began this work, the task of identifying individual genes contributing to quantitative trait expression was thought to be literally impossible. The long-standing assumption about such quantitative traits was that the contributing genetic influences were due to large numbers of genes with individually small, interchangeable effects. Identifying one or several genes from among this group was not thought feasible. Description of such traits was limited, therefore, to focusing on overall effects, like phenotypic variance and the pattern of responses to artificial selection. But he and his students, such as S. G. Spickett, pioneered innovative experimental designs that overcame the limitations set by these generalizations (17, 26). They were able to identify a small number of genes that contributed in distinct ways to the development of sensory bristles in *Drosophila*. In this way, they established a new avenue to explore the genetic basis of complex traits by locating these ‘polygenes’ and studying the way individual members of the quantitative genetic system worked (25, 27, 35, 36, 40). This identification of contributing genetic loci opened up such quantitative traits for more in-depth developmental analysis (37). While many gene loci might potentially contribute to the phenotype in minor ways, a small number of genes could be found to account for most of the quantitative variation for a clearly-defined trait. For example, even though a character such as ‘overall size’ might be influenced by hundreds of genes, a more sharply-defined quantitative character, such as bristle number on the thorax, was open to more in-depth analysis of fly-to-fly variation in factors such as bristle cell division rates and positional distribution on the thorax. Even a few of these genetic loci of small effect could have large influences on the development of the character (5, 7).
Acceptance of his ideas did not always come quickly; many challenged the idea that quantitative characters could have a simpler genetic basis than originally assumed from mathematical models. But the very existence of the disagreement simply confirms that Thoday was attracted to ideas that had the potential to change the landscape of our knowledge in ways that the gradual accumulation of new facts would not. Although the polygenic factors influencing bristle numbers in *Drosophila* were not characterized in detail, their very identification provided a proof of principle. The view that complex traits could be influenced by variation in a few contributing genes gained acceptance, although the characterization of such factors had to wait until methods for rapid DNA sequencing and screening were developed. Early perspectives are explored in *Quantitative genetic variation* (37), and the study of polygenes, now more familiar as quantitative trait loci, plays a fundamental role in fields ranging from human and medical genetics to agriculture and plant breeding.

Perhaps John Thoday’s biggest contribution was in highlighting the critical importance of genetic differences among individuals in understanding how biology and evolution might operate. In 1953 he published an important paper on the genetic components of fitness (4). ‘Fitness’ in this context is defined as the probability for evolutionary survival. From this perspective, he led an extensive study to explore a controversial form of genetic response to selection: disruptive selection. In a large series of papers on disruptive selection, he explored potential mechanisms and consequences (6, 8–10, 12), often in collaboration with his colleagues and graduate students, including T. B. Boam (11, 14, 16), E. Millicent (13, 15), J. B. Gibson (18, 19, 23, 24, 33, 39), D. R. Wolstenholme (22), D. O. F. Skibinski (38) and C. G. N. Mascie-Taylor (39). He reviewed this work in an address to the Royal Society in 1972 (31). He was a skilled and insightful experimentalist. His research designs were often simple and elegant. At that time, the commonly-held view of genetic change in natural populations assumed that selection depended on relative reproductive success among genetically different members of a reproductively integrated population. For more than one type to be favoured at the same time required some form of reproductive isolation. Thus, models were often built on geographical separation into subpopulations. But Thoday believed that other factors could support reproductive isolation among groups within a single location. He considered examples such as temporal separation of reproductive activity resulting, for example, from different pollinators in plants or taking advantage of environmental heterogeneity. Examples might include shifts in plant flowering time that occur in response to pollinator habits or an insect species taking advantage of environmental heterogeneity by one group seeking sunny spaces while another group favour nearby darkened forest habitats. Results of this heterogeneity of behaviour could have effects ranging from polymorphism to speciation. The existence of this disruptive selection was controversial, and was sometimes criticized when other researchers were unsuccessful in replicating his results. Thoday and his colleagues pointed out weaknesses in other experimental designs, but it is also likely that Thoday was lucky in working with a genetically diverse fruit fly population, which contained the resources of genetic variation to respond to his experimental designs. It is now recognized that disruptive selection can be a force acting in some populations. But perhaps more significantly, it shows that a creative mind that is not constrained by current beliefs, but that is open to new ways of looking at old problems, can discover interesting truths.

The peak of his research output occurred at a time of great productivity in genetics. It was a period of significant innovation in the technology and methods applied to research in genetics and allied disciplines. In his academic role at Cambridge, Thoday actively promoted...
curriculum development, thus increasing the role of genetics in teaching biology at Cambridge and expanding the department’s activity in areas such as molecular biology. Thoday and a few others stood out because they were not merely insightful experimentalists but also philosophers of the subject. He, perhaps more than many of his contemporaries, was able to fit new discoveries in genetics into their broader biological contexts. In particular, he was deeply concerned with the wider societal implications of genetic variation between humans. The nature versus nurture debate has existed since the beginning of genetics and has always been beset by extreme views on both sides. John Thoday’s research gave him a deep understanding of the complex interactions that exist between genetic variation and environmental variation in all living organisms. This understanding, and perhaps also the experience of his war service, made him despair equally of the genetic determinism of the eugenicists and, of those who contended that environment lay at the root of society’s problems (28–30, 32).

His views, and his essential humanity, are perhaps best illustrated by a couple of quotations from his review of a book on educability and group differences, written by Arthur Jensen (34): ‘individuals, however malleable, are different and should not be treated as if they were the same’; ‘no demonstration that a group difference has a genetic component could justify racism’.

From individual genes in a quantitative genetic array to the role of a genetic perspective on issues such as education, social mobility and human population structure, few at his time took such a broad and holistic view of genetics as did John Thoday.

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AUTHOR PROFILES

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Don MacDonald was a lecturer in the Department of Genetics, Cambridge, from 1975, and was a colleague of Professor John Thoday until the latter’s retirement in 1983. He then served as head of the Department of Genetics from 1991 until 1992 and again from 1996 until 1999, before becoming director of Medical and Veterinary Education in the Faculty of Biology from 2000 until retirement in 2010. He was elected to a fellowship of Wolfson College, Cambridge, in 1994, and served as vice president of the College from 2007 to 2011.
James N. Thompson Jr is David Ross Boyd Professor of Biology at the University of Oklahoma. He entered the University of Cambridge in 1970 as a Marshall Scholar to study with Professor Thoday on genetic mechanisms of quantitative variation in development, using \textit{Drosophila} as a model organism. After earning his PhD in 1973, he continued that work supported by an SRC grant to Professor Thoday, before accepting a position on the faculty of Zoology at the University of Oklahoma in 1975. There he teaches courses in genetics, introductory zoology (honours) and advanced subjects, and he served for 19 years as chair of that department. Collaboration continued with Professor Thoday, to include co-editing \textit{Quantitative genetic variation} (37), published in 1979 by Academic Press, London.

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