

Conrad Hal Waddington (1905-1975) ^[1]

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[Conrad Hal Waddington](#) ^[5] was an embryologist and theoretical biologist. His early experimental work investigated aspects of embryonic [induction](#) ^[6] and the properties of the [organizer](#) ^[7] first identified by [Hans Spemann](#) ^[8] and [Hilde Mangold](#) ^[9], while his later studies focused on [genetic assimilation](#) ^[10]. Waddington is probably best known for developing the concept of the [epigenetic landscape](#) ^[11], and he also held significant interest in many different areas ranging from the visual arts and poetry to philosophy. Throughout his career, Waddington maintained that the arts were integral to science, and he continued to draw inspiration from the arts for his own work.

[Conrad Hal Waddington](#) ^[5] was born on 8 November 1905 in Evesham, England, to Mary Ellen Warner and Hal Waddington. Waddington's father was a tea planter in South India. His family life was difficult; for instance he did not see his father between the ages of five and fifteen years old due to [World War I](#) ^[12], which caused a disruption in travel between Britain and India. Waddington attended Clifton College School where he was introduced to Eric J. Holmyard, a chemistry textbook writer. In addition to science, Holmyard introduced Waddington to metaphysics such as Arabic alchemy and Alexandrian Gnosticism.

After high school, Waddington attended the Sydney Sussex College at the University of Cambridge, where he studied the natural sciences, focusing on geology. Waddington had a reputation for being idiosyncratic; rather than completing his required course work, for instance, he spent his time reading the philosophy of Alfred North Whitehead. In 1926 Waddington graduated with first class honors from the University of Cambridge. In the same year, he married ?Lass? Lascelles, with whom he had one son. Later in his life Waddington admitted that he was more interested in poetry than science throughout his undergraduate degree. Also in 1926, Waddington began graduate school at Cambridge focused on paleontology, especially in ammonites. Quite typically for him he held two studentships during his graduate degree, one in geology, the other in philosophy.

Waddington left Cambridge in 1929 without finishing his doctoral thesis. He received a ScD in 1938 on the merit of his published work. His first appointment was a research fellowship at the [Strangeways Research Laboratory](#) ^[13], where he published his investigation of the genetics of germination in *Matthiola*. In 1930 Waddington became a demonstrator in zoology at Cambridge through a part-time grant from [Medical Research Council](#) ^[14] for his culture work at Strangeways. Waddington also received a Rockefeller Research Fellowship, which allowed him to spend six months in Freiburg, Germany, with [Hans Spemann](#) ^[8].

During his time at Strangeways, Waddington began to study embryonic development in higher mammals. He was able to show the presence of the [organizer](#) ^[7] in higher mammals and [birds](#) ^[15]. One of his most celebrated experiments was the face to face joining of two [duck](#) ^[16] blastoderms. This induced a second [primitive streak](#) ^[17] in the [blastoderm](#) ^[18], demonstrating the inductive effects of that structure. In 1933 he became a lecturer of zoology at [Strangeways Research Laboratory](#) ^[13] under the director, Honor Fell. In that same year, Waddington was

named a Fellow at Christ's College. In work published in 1934, Waddington was able to transplant the [primitive streak](#) [17] from a [chick](#) [19] to a [rabbit](#) [20] embryo, inducing a second axis in the [rabbit](#) [20] embryo. Subsequently, Waddington worked with [Joseph Needham](#) [21] on chemical [induction](#) [6] in [amphibians](#) [22]. In 1936 divorce ended his first marriage. The same year he married the architect Justin Blanco White, with whom he had two daughters. As part of his interest in theoretical questions of biology, Waddington joined the Theoretical Biology Club in the late 1930s.

In 1939 Waddington traveled to the United States, where he worked at the [California Institute of Technology](#) [23] with [Alfred Sturtevant](#) [24] and [Theodosius Dobzhansky](#) [25] researching [Drosophila](#) [26]. In 1940, after he left the Theoretical Biology Club, Waddington joined a scientific dinner club called "Tots and Quots." The purpose of this club was to promote the use of science in war. World War II had broken out the year before. As Britain was drawn into the war, Waddington contributed to a book, *Science in War*. His contribution was a chapter titled, "Meat at Any Price," which promoted the use of science to analyze military operations in order to improve their effectiveness. Waddington spent some time with the Royal Air Force and improved German U-boat detection measures through the use of mathematical modeling. His paper, "Operational Research Against the U-Boat," was written in 1946 for the Royal Air Force Coastal Command but was not published until 1973.

Waddington's book, [Organisers and Genes](#) [27], was published in 1940. There he described the concept of [competence](#) [28], which is the ability of a given cell or tissue to react to an inducing signal. He also proposed the concept of the [epigenetic landscape](#) [11], which would reappear in many of his later publications as a model of tissue [determination](#) [29]. After the war, Waddington became the Chair of Genetics at Edinburgh in 1945. The same year, he also became the Chief Geneticist for the National Animal Breeding and Genetics Research Organization. For his fiftieth birthday, his colleagues threw him a surprise birthday party with a pinball machine constructed as an [epigenetic landscape](#) [11]. His book, [The Strategy of the Genes](#) [30], which further describes the [epigenetic landscape](#) [11], was published in 1957. The [epigenetic landscape](#) [11] is a visual metaphor of a ball signifying a cell, traveling down a landscape of ridges and valleys where multiple factors influence the cell to take a certain course toward a final tissue type. Waddington also included the activity of [genes](#) [31] in his model. The [genes](#) [31] were able to pull on the strings, or "chreodes" as he named them, which Waddington envisioned creating the developmental pathways a cell may take.

Waddington's studies in genetics led him to the idea of [genetic assimilation](#) [10]. He proposed this as a Darwinian mechanism that allows certain acquired characteristic to become heritable. This work was important to refute the work of Trofim Denisovich Lysenko, the agricultural scientist who was forcing the idea of acquired characteristics onto Soviet genetics. Waddington focused his [genetic assimilation](#) [10] work on the crossveinless trait of [Drosophila](#) [26]. This is a trait that occurs with high frequency in heat-treated flies. After a few generations, the trait can be found in the population, without the application of heat, based on hidden genetic variation that has been "assimilated."

Later in his career, Waddington focused more on theoretical biology, organizing four symposia on the subject of theoretical biology. These symposia helped to generate several ideas, such as the Positional Information Theory by [Lewis Wolpert](#) [32]. Waddington also helped to found the International Biological Program, a five year study into many aspects of the interaction between [humans](#) [33] and biology throughout the world in 1964. In 1970 Waddington accepted the position of the Albert Einstein Chair in Science at the [State University of New York in Buffalo](#) [34].

Waddington won many awards for his varied academic pursuits. He became a Fellow of the Royal Society of Edinburgh in 1947. He was named to the Finnish Academy in 1957. He was named a Commander of the Order of the British Empire in 1958. In 1959 Waddington became a foreign member of the [American Academy of Arts and Sciences](#) [35]. He also was a Fellow of the Deutsche Akademie der Naturforscher Leopoldina, the oldest scientific academy in Germany (founded in 1677). He was awarded honorary ScD from the University of Montreal in 1958; Trinity College, Dublin, in 1965; Prague in 1966; and Geneva in 1968. He also received an LLD from Aberdeen in 1966.

Waddington died on 26 September 1975 of a heart attack at sixty nine years of age.