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**Conrad Hal Waddington** - In the early 1930s, Waddington and many other embryologists looked for the molecules that would induce the amphibian neural tube. The search was beyond the technology of that time, and most embryologists moved away from such deep problems. Waddington, however, came to the view that the answers to embryology lay in genetics, and in 1935 went to [Thomas Hunt Morgan's](https://en.wikipedia.org/wiki/Thomas_Hunt_Morgan) *Drosophila* laboratory in California, even though this was a time when most embryologists felt that genes were unimportant and just played a role in minor phenomena such as eye colour.

In the late 1930s, Waddington produced formal models about how gene regulatory products could generate developmental phenomena, showed how the mechanisms underpinning *Drosophila* development could be studied through a systematic analysis of mutations that affected the development of the [*Drosophila*](https://en.wikipedia.org/wiki/Drosophila) wing. In a period of great creativity at the end of the 1930s, he also discovered mutations that affected cell phenotypes and wrote his first textbook of "developmental epigenetics", a term that then meant the external manifestation of genetic activity.

Waddington introduced the concept of [canalisation](https://en.wikipedia.org/wiki/Canalisation_%28genetics%29%22%20%5Co%20%22Canalisation%20%28genetics%29), the ability of an organism to produce the same [phenotype](https://en.wikipedia.org/wiki/Phenotype) despite variation in genotype or environment. He also identified a mechanism called [genetic assimilation](https://en.wikipedia.org/wiki/Genetic_assimilation) which would allow an animal's response to an environmental stress to become a fixed part of its developmental repertoire, and then went on to show that the mechanism would work.

In 1972, Waddington founded the Centre for Human Ecology in the [University of Edinburg](https://en.wikipedia.org/wiki/University_of_Edinburgh) Waddington's [epigenetic landscape](https://en.wikipedia.org/wiki/Epigenetic_landscape) is a metaphor for how [gene regulation](https://en.wikipedia.org/wiki/Regulation_of_gene_expression) modulates development. Among other metaphors, Waddington asks us to imagine a number of marbles rolling down a hill. The marbles will sample the grooves on the slope, and come to rest at the lowest points. These points represent the eventual [cell](https://en.wikipedia.org/wiki/Biological_cell) fates, that is, [tissue](https://en.wikipedia.org/wiki/Biological_tissue) types. Waddington coined the term [chreode](https://en.wikipedia.org/wiki/Chreode%22%20%5Co%20%22Chreode) to represent this cellular developmental process. The idea was based on experiment: Waddington found that one effect of mutation (which could modulate the epigenetic landscape) was to affect how cells differentiated. He also showed how mutation could affect the landscape, and used this metaphor in his discussions on evolution—he emphasised (like [Ernst Haeckel](https://en.wikipedia.org/wiki/Ernst_Haeckel) before him) that evolution mainly occurred through mutations that affected developmental anatomy.



Waddington proposed an evolutionary process, "[genetic assimilation](https://en.wikipedia.org/wiki/Genetic_assimilation)", as a [Darwinian](https://en.wikipedia.org/wiki/Darwinian) mechanism that allows certain acquired characteristic to become heritable. According to Navis, (2007) "Waddington focused his genetic assimilation work on the crossveinless trait of [*Drosophila*](https://en.wikipedia.org/wiki/Drosophila). This trait 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 Waddington asserted had been "assimilated" Other biologists such as [Wallace Arthur](https://en.wikipedia.org/wiki/Wallace_Arthur) disagree, writing that "genetic assimilation, looks, but is not Lamarckian. It is a special case of the evolution of [phenotypic plasticity](https://en.wikipedia.org/wiki/Phenotypic_plasticity)".[[18]](https://en.wikipedia.org/wiki/C._H._Waddington#cite_note-wallace-evo-19) Adam S. Wilkins wrote that "[Waddington] in his lifetime... was widely perceived primarily as a critic of Neo-Darwinian evolutionary theory. His criticisms ... were focused on what he saw as unrealistic, 'atomistic' models of both gene selection and trait evolution." In particular, according to Wilkins, Waddington felt that the Neo-Darwinians badly neglected the phenomenon of extensive gene interactions and that the "randomness" of mutational effects, posited in the theory, was false

**Thomas Hunt Morgan-** n 1890, Morgan was appointed associate professor (and head of the biology department) at Johns Hopkins' sister school [Bryn Mawr College](https://en.wikipedia.org/wiki/Bryn_Mawr_College), replacing his colleague [Edmund Beecher Wilson](https://en.wikipedia.org/wiki/Edmund_Beecher_Wilson).[[8]](https://en.wikipedia.org/wiki/Thomas_Hunt_Morgan#cite_note-8) Morgan taught all morphology-related courses, while the other member of the department, [Jacques Loeb](https://en.wikipedia.org/wiki/Jacques_Loeb), taught the physiological courses. Although Loeb stayed for only one year, it was the beginning of their lifelong friendship. Morgan lectured in biology five days a week, giving two lectures a day. He frequently included his recent research in his lectures. Although an enthusiastic teacher, he was most interested in research in the laboratory. During the first few years at Bryn Mawr, he produced descriptive studies of [sea acorns](https://en.wikipedia.org/wiki/Sea_acorn), ascidian worms, and frogs.

In 1894 Morgan was granted a year's absence to conduct research in the laboratories of *[Stazione Zoologica](https://en.wikipedia.org/wiki/Stazione_Zoologica%22%20%5Co%20%22Stazione%20Zoologica)* in [Naples](https://en.wikipedia.org/wiki/Naples), where Wilson had worked two years earlier. There he worked with German biologist [Hans Driesch](https://en.wikipedia.org/wiki/Hans_Driesch), whose research in the experimental study of development piqued Morgan's interest. Among other projects that year, Morgan completed an experimental study of [ctenophore](https://en.wikipedia.org/wiki/Ctenophore) embryology. In Naples and through Loeb, he became familiar with the *Entwicklungsmechanik* (roughly, "developmental mechanics") school of experimental biology. It was a reaction to the vitalistic *[Naturphilosophie](https://en.wikipedia.org/wiki/Naturphilosophie%22%20%5Co%20%22Naturphilosophie)*, which was extremely influential in 19th-century morphology. Morgan changed his work from traditional, largely descriptive morphology to experimental embryology that sought physical and chemical explanations for organismal development. At the time, there was considerable scientific debate over the question of how an embryo developed. Following [Wilhelm Roux](https://en.wikipedia.org/wiki/Wilhelm_Roux)'s mosaic theory of development, some believed that hereditary material was divided among embryonic cells, which were predestined to form particular parts of a mature organism. Driesch and others thought that development was due to epigenetic factors, where interactions between the protoplasm and the nucleus of the egg and the environment could affect development. Morgan was in the latter camp; his work with Driesch demonstrated that [blastomeres](https://en.wikipedia.org/wiki/Blastomeres) isolated from [sea urchin](https://en.wikipedia.org/wiki/Sea_urchin) and ctenophore eggs could develop into complete larvae, contrary to the predictions (and experimental evidence) of Roux's supporters. A related debate involved the role of [epigenetic](https://en.wikipedia.org/wiki/Epigenetic) and environmental factors in development; on this front Morgan showed that [sea urchin](https://en.wikipedia.org/wiki/Sea_urchin) eggs could be induced to divide without fertilization by adding [magnesium chloride](https://en.wikipedia.org/wiki/Magnesium_chloride). Loeb continued this work and became well-known for creating fatherless frogs using the method. When Morgan returned to Bryn Mawr in 1895, he was promoted to full professor. Morgan's main lines of experimental work involved [regeneration](https://en.wikipedia.org/wiki/Regeneration_%28biology%29) and larval development; in each case, his goal was to distinguish internal and external causes to shed light on the Roux-Driesch debate. He wrote his first book, *The Development of the Frog's Egg* (1897). He began a series of studies on different organisms' ability to regenerate. He looked at grafting and regeneration in tadpoles, fish, and earthworms; in 1901 he published his research as *Regeneration*.

Beginning in 1900, Morgan started working on the problem of [sex determination](https://en.wikipedia.org/wiki/Sex-determination_system), which he had previously dismissed when [Nettie Stevens](https://en.wikipedia.org/wiki/Nettie_Stevens) discovered the impact of the Y chromosome on sex. He also continued to study the evolutionary problems that had been the focus of his earliest. In *A Critique of the Theory of Evolution* (1916), Morgan discussed questions such as: "Does selection play any role in evolution? How can selection produce anything new? Is selection no more than the elimination of the unfit? Is selection a creative force?" After eliminating some misunderstandings and explaining in detail the new science of Mendelian heredity and its chromosomal basis, Morgan concludes, "the evidence shows clearly that the characters of wild animals and plants, as well as those of domesticated races, are inherited both in the wild and in domesticated forms according to the Mendel's Law". "Evolution has taken place by the incorporation into the race of those mutations that are beneficial to the life and reproduction of the organism". Injurious mutations have practically no chance of becoming established.