new interpretations.” Indeed, when Beadle left the fly group and started serious work in biochemical genetics, he was quite shocked at the cut-throat competitive nature of the biochemistry community, compared to the much more cooperative attitude of Drosophila geneticists, who readily shared ideas, data and biological materials amongst themselves (to some extent this is still true of fly workers, especially in evolutionary genetics). In the present time of secrecy, proprietary rights and patents in much of biology, this is perhaps an important legacy of Morgan that we should try hard not to lose track of. Science is ultimately a collective endeavour and knowledge is a gift to be shared freely, not a resource to be hoarded or an investment to be protected.

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Thomas Hunt Morgan and Developmental Biology

Thomas Hunt Morgan was in the unique position of being able to combine genetics and developmental biology and create the discipline of developmental genetics. Yet, the latter field came of its own much later, in the 1970s, over 40 years after Morgan won the Nobel Prize. What took it so long? Morgan’s training and the science of his times give us one perspective, which only adds to the puzzle.

We know rather little about how complex functions of organisms – such as processing visual information or the ability for abstract thought – are related to the physiology of the brain. We know even less about how these functions emerge during development. And, we know the least about the roles of genes in either of these two processes. Of course, genes play an all-encompassing role at a rather obvious and trivial level. Organisms are the consequences of the function of their cells and cellular-constituents; and since genes encode proteins, and the function of proteins affects the function of cells, ergo, genes determine everything, including how one reacts to the environment. Looked at in this apparently ‘trivial’ way, developmental genetics is merely the use of the scalpel of genetics to study developmental biology. However, in practice, it has been an intellectually stimulating discipline in its own right, in addition to being of practical value in understanding developmental mechanisms.

The golden period of embryology was in the 19th and early 20th century with much of the action centered in Europe, principally in Germany. Many American researchers went to Europe and interacted closely with colleagues there and experimental embryology developed rapidly in the USA. Morgan got his PhD on the evolutionary relationships of pycnogonids (sea spiders) at Johns Hopkins University and was an expert in zoology. This choice of career developed from an early interest in wildlife. As a young child of ten, he collected birds, birds’ eggs, and fossils and after his undergraduate studies spent some time in a marine laboratory. He succeeded the famous cell biologist E B Wilson, who influenced him greatly, at Bryn Mawr College in 1891, a well-known women’s college where Morgan met his future wife (Lilian Sampson, a student, embryologist and his collaborator for some years).
Morgan's interests soon moved from morphology to experimental embryology. He worked on regeneration in earthworms and the development of sea urchins. Hans Driesch, whom Morgan met at the Naples Zoological Station, became a friend. Driesch himself became a vitalist—someone who did not believe that all phenomena have a material basis and explanation—after his famous experiment with the sea urchin embryo. August Weismann had proposed (and I state this in today's language) that the asymmetric segregation of regulatory factors to daughter cells was a mechanism by which sibling cells could adopt different cell-fates. Wilhem Roux tested Weismann's hypothesis by ablating one cell of a tadpole embryo at the two-cell stage and showed that only half an animal was formed, consistent with Weismann's hypothesis. Driesch separated the two-cells of a sea urchin embryo and found that each could make an entire animal, contrary to Roux's results. Seeing no obvious material basis for his results, Driesch became a vitalist-philosopher. These experiments are well known, but what is not is that Morgan himself performed another experiment that went against Weismann's hypothesis of asymmetric segregation of determinants and showed that the 'protoplasm' at the two-cell stage was not as different as Roux's experiments suggested. Morgan and Driesch interacted closely, though Morgan was by no means a vitalist. Driesch and he agreed though on the importance of experiments and their proper design.

In his later years at Columbia University and at the California Institute of Technology, Morgan of course devoted much of his time to genetics, but continued his interest in embryology. Two major contributions stand out as perceptive and valuable even today. The first was from his early work on the earthworm and the second on his later study on regeneration.

Morgan's earthworm experiments were possibly the first clear statement about the idea of a 'morphogen' that acts at a distance to specify the fate of cells. These were, till recently, hypothetical soluble molecules, which could travel many cell-diameters away from their source by diffusion and alter cell-fate in a concentration dependent manner. By examining regeneration in the earthworm, Morgan suggested that the head region had an anterior-producing substance that acted on cells to cause anterior structures to be made. In these experiments, Morgan also linked the mechanisms used in regeneration to those used in normal development. Morgan examined regeneration in detail and wrote a book on the subject based on his work. There was a view that regeneration was an adaptation to repair damage. An example given was the regeneration of damaged claws in the hermit crab. Morgan showed that body parts that were not usually damaged, such as the abdomen, could also regenerate. The field of regeneration is one of the most exciting today in developmental biology and the molecular mechanisms are only now being addressed.

The late 19th and early 20th century saw the advent of two major changes in biology. These were the theory of evolution by natural selection of Darwin and Wallace, and the discovery of Mendel's laws and the growth of genetics. Morgan was interested in evolution, but did not accept Darwinism. He thought more work was needed and was particularly skeptical of the mechanisms proposed by Darwin for speciation. The Mendelian geneticists and Darwinians did not agree with each other at all. The Darwinians did not appreciate how drastic changes caused by...
mutation could account for the comparatively slow rate of speciation. Morgan, interestingly, was not comfortable with either Mendelian genetics or the chromosomal theory of heredity. These views are amazing—they show the critical and skeptical nature of the man. But, they also show how drastically he changed his views later, on the basis of results from superbly designed experiments whose interpretation depended greatly on his training as an embryologist. The work of an undergraduate, Alfred Sturtevant, in Morgan’s fly room resulted in the first gene-linkage map. Morgan’s training as a cytologist soon allowed him to see that the four linkage groups in *Drosophila* corresponded to the four cytologically identifiable pairs of chromosomes. Thus Morgan, initially skeptical about the role of chromosomes, showed that genes were on chromosomes.

Morgan’s training in, and contribution to, embryology, his founding *Drosophila* genetics and his clear statements that genes must play roles in development would lead one to think that his school would have pioneered the field of developmental genetics in his lifetime—much, if not all the tools were already available. Morgan wrote a book on embryology and genetics, with an idea to unify the two fields. But, in reality, the book was two books in one—one on embryology and one on genetics, with not too much of a link between them. Developmental genetics took longer to develop. Derek Poulson at Caltech and then at Yale pioneered the field with the study of deletions of a locus, Notch, in *Drosophila*, that caused overgrowth of the nervous system. Others, Salome Gluecksohn-Wealsch and C F Waddington, working in the laboratory of Hans Speman, were other pioneers working on mice and flies respectively. But these efforts were relatively isolated as were several other significant ones. It was only in the 1970s that Morgan’s embryology and genetics were integrated. This had to wait for the work of Edward Lewis (a student of Morgan’s student, Alfred Sturtevant), Antonio Garcia-Bellido (inspired by a sabbatical in Morgan’s home, Caltech) and co-workers, Peter Lawrence and finally the *tour de force* of Christiane Nusslein-Volhard and Eric Weischaus in Heidelberg. These workers combined the power of *Drosophila* genetics with insightful experiments to establish how gene activity was a critical player in animal development. Their work also gave us insights on the molecular nature of developmental mechanisms. What took so long? Make your guess!

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"The most significant addition that have been made to Mendel’s two laws may be called linkage and crossing-over.... By further extension and clarification of this idea, it became possible, as more evidence accumulated, to demonstrate that the genes lie in a single line in each chromosome."

—*T H Morgan, Nobel Lecture*