Conrad Waddington and the Marriage of Genetics, Development, and Evolution

C H Waddington was an important figure in the early days of linking development and the genetics of development with the study of evolution. There had been great advances in embryology from the 19th century onwards and going well into the 20th. It all started with the simple description of the development of a wide variety of animals and was followed by the beginning of experimental analysis, led by Wilhelm Roux, who pushed for understanding the mechanics of development – how and why one step led to the next. Later this was called 'causal embryology'. It culminated in the early 20th century when Hans Spemann and Hilda Mangold discovered the amphibian "organizer" where one part of an embryo induced another part to form the main axis of the embryo.

As has been pointed out by various authors, all this beautiful work took place with little or no regard to evolution. It is true that Ernst Haeckel, in the latter part of the 19th century, made some bold strokes to bring the two together, but the time was not right and his ideas were pushed aside and buried under a heap of not very profound objections. (Furthermore Darwin, in his *Origin*, tied in embryological development in the great scheme of evolution.) Aside from the important realization at the turn of the century that the chromosomes of all cells carry Mendel's genetic factors, there was no major linking of development with genetics, or for that matter any genetics before 1900!

The principal pioneer who brought the two together was Waddington. In 1940 he published his *Organizers and Genes* and the ideas he spread grew to be of considerable importance. Genetics itself strayed from embryology because of the great success of population genetics – how the frequencies of particular genes changed in an evolving population. It proved to be a powerful approach, but one that had no relevance to embryology; the two subjects had gone on quite separate ways, neither one needing nor heeding the other. Waddington and a few other notable workers such as Schmalhausen changed all that. The construction of an organism, from fertilized egg to the formation of the embryo and the adult, involved genetic instructions to lay out the internal changes necessary for reaching maturity. The outcome that followed this modest beginning has been enormous, mostly because of the advent of molecular biology. From mid 20th century onwards, the genetics of development became a gigantic and very successful industry. We can now dissect the steps of development to the finest detail, from the genes to their effect on the developing cells to the organization of the ultimate body plan. Waddington had laid down the foundation.

In 1957, I went to Scotland on a sabbatical leave to work in Waddington's Institute of Animal Genetics at the University of Edinburgh. It was an exhilarating experience for many reasons, from the trivial to the important. I was working on slime molds and made the trivial discovery that the central heating in the building was turned off at noon on Saturday and back on Monday morning. It meant that all my slime molds on the laboratory bench stopped in their tracks and did not resume their activities until mid-morning on Mondays. We all had the weekend off!

The non-trivial and important part of my visit was the remarkable intellectual environment. Waddington had gathered a most distinguished group of scientists in his Institute, and I had a large number of stimulating interactions with many of them. This was greatly helped by there being a small lunchroom in the building and genetics, embryology and many other aspects of biology were much discussed there. I also had numerous conversations with Waddington. He would tour the building and talk to each of the researchers; he kept his hand on the pulse of the Institute. He visited me on these tours, much to my profit.

He was a man of considerable reserve, but when discussing science he was free and open, and would discuss everything from problems with the mechanics of an experiment to the deeper implications. Besides running the Institute he was extremely prolific, not only writing up experiments, but writing on diverse subjects. I remember being with him at a conference where we listened to talks all day and during the break before dinner I passed his window and heard his typewriter clacking away. Afterwards I asked him what he was doing when we were all relaxing and he said he was working on a chapter of a book he was writing; no rest needed!

Often we would discuss bigger biological issues and his insights were often sharp and deep. It was a long time ago, but I do remember one discussion where he felt quite passionately. He was totally down on population genetics, even though some of the leading workers in the field were in his Institute and with whom he got along well. As I pointed out earlier, population genetics totally ignored development. But he would go beyond this in his zeal to bring all of evolution into one tent, with embryology playing a major role. He would ask, rather aggressively, "What significant contribution has population genetics made"? He clearly thought none. In his writing he concentrated on genetics and development as the key parts of evolutionary biology. He had an original mind full of fresh ideas, and he had the energy, and particularly the skill to express them on paper with enviable penetration and clarity.

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