Walter J Gehring (1939–2014)

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Professor Emeritus Walter J Gehring. Photograph courtesy of The Biozentrum, University of Basel.

The scientific community has been deeply saddened by the passing of Walter Gehring on May 29 as a result of injuries from a tragic car accident. Walter was an eminent figure and renowned developmental biologist with a passionate curiosity, an infectious enthusiasm for all aspects of biology, a deep drive to discover fundamental concepts, and visionary ideas that inspired young and old across disciplines. Walter Gehring is probably best known for the discovery of the homeobox in 1984, a gene segment encoding the evolutionarily conserved DNA-binding homeodomain, which is present in many related transcription factors such as the homeotic proteins and *Hox* genes that specify different regions along the anterior–posterior body axis in animals throughout the animal

kingdom. His second major impact was the discovery of the conserved function of the *eyeless/Pax6* gene family in eye development, leading to the pioneering concept that corresponding organs in different animals are specified by conserved transcription factors.

Walter was born in Zurich, Switzerland, where he studied Zoology and obtained his PhD under the guidance of Ernst Hadorn. Already then, his model organism of choice was the fruit fly *Drosophila melanogaster*. His thesis work focused on ‘transdetermination’ of imaginal disks, in today’s world maybe a somewhat esoteric phenomenon, but back then in the pre-molecular days, a highly modern approach. Transdetermination describes the observation that imaginal disks, epithelial sacs that are the precursors

of adult external structures, can change their fate, for example transforming a leg imaginal disk into one that gives rise to an antenna or a wing, after culturing it in adult hosts. Walter realized that understanding transdetermination would reveal processes that underlie the specification of different body parts. Coincidentally, he discovered an allele of the homeotic gene *Antennapedia*, a genetic lesion that transforms antennae into legs, which later crystalized into the ‘fil rouge’ of his career. In 1965, he joined as a postdoctoral fellow Alan Garen at Yale University, where he was quickly promoted to Assistant and then to Associate Professor of Developmental Biology. In 1972, Walter returned to Switzerland and joined the newly founded Biozentrum of the University of Basel, where he served as Chair and Professor of Cell Biology until his recent retirement.

Walter’s research interests centered on the mechanisms by which cells and organs of a developing embryo acquire their fate and are specified in the correct place, thus properly forming organs in the adult organism. Although Walter worked with worms, squids, ascidians, and other animals, *Drosophila* remained his favorite experimental organism and he skillfully tailored his experimental strategies to take full advantage of the ever evolving molecular, genetic, and genomic arsenal to dissect and elucidate fundamental questions in biology.

The work in his group culminated in many seminal discoveries. Early in his independent career, his group cloned the *Antennapedia* gene, which served as an entry point to decipher the molecular mechanisms of homeotic transformation and resulted in the discovery of the homeobox. Walter followed through on the homeobox discovery and found that the homeodomain is a DNA-binding domain and later described

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DOI 10.15252/embj.201489291

the homeodomain protein structure and how it binds to DNA. Notable is also his discovery of the evolutionarily conserved, organogenesis-regulating genes of the *eyeless/Pax6* family, which act as master control genes for eye development across the animal kingdom directing the development of very different types of eyes such as the single lens eyes of vertebrates and the facet eyes of insects. He interpreted this surprising discovery to indicate that the various eyes found in the animal kingdom evolved from a single ancestral eye. The notion that eyes have a common evolutionary origin transformed the way we think about the evolution of organs and body plans, and his recent work addressed the conundrum of how the morphologically distinct eyes of insects, octopi, and vertebrates evolved from a common ancestor. All these discoveries opened up new fields of research, and others later found that these concepts hold true for many other organs and developmental processes.

His group also pioneered numerous molecular and genetic techniques such as *in situ* hybridization, revealing striped segmental expression of homeobox and other genes, and enhancer trapping, which is used to discover new genes and to dissect genetic regulatory networks. In general, he immediately recognized and implemented novel techniques before they became common practice, for example DNA/gene cloning and associated molecular genetics. The discovery of a conserved DNA element,

the homeobox, in several body axis patterning genes, was a quantum leap in molecular developmental biology, as it suddenly made cloning of additional such genes in *Drosophila* and other animal species easy via homology DNA hybridization. Although Walter is known for his work with *Drosophila*, he was passionate about zoology and developmental biology in general. As a manifest of that, every summer he directed a marine biology course at the Laboratoire Arago (L'observatoire Océanologique) in Banyuls in the south of France, where a minilab was set up and participants performed experiments with sea urchins, ascidians, and other animals that they collected from the Mediterranean.

Walter's outstanding research contributions were recognized by many prestigious awards from around the world, including the Jeantet Prize for Medicine (1987), the March of Dimes Prize in Developmental Biology (1997), the Kyoto Prize for Basic Science (2000), and the Balzan Prize for Developmental Biology (2002). He was also honored with the "Grosses Bundesverdienstkreuz" of the Federal Republic of Germany in 2010 and was elected to several national academies, including the Royal Society of London and the US National Academy of Science. Walter acted as president of the International Society for Developmental Biologists (ISDB) and as secretary-general of the European Molecular Biology Organization (EMBO).

It is impossible to view Walter's impact on developmental biology only through his own work, as he inspired numerous researchers, and many of his former students and postdocs have become leaders in their own right. Indeed, Walter had a gift of recruiting highly talented and ambitious people and his laboratory was a buzzing group of researchers who were driven to make groundbreaking discoveries. Not only that, but Walter also had a sharp instinct and determination to push some initially crazy ideas of which many eventually were proven correct. Throughout his life, Walter kept close contact with his former trainees and collaborators around the world and he indeed founded a large and cohesive scientific family, spanning diverse disciplines and model organisms. It was only a couple of months ago in March, when many of us attended a symposium in Basel to honor him on his 75th birthday, where Walter was in great spirits and full of energy and enthusiasm. This was the last of several such meetings, which exemplified his impact on biology and many of us, and where his former students and coworkers gathered to celebrate and exchange scientific ideas and social memories.

Walter Gehring was an extraordinary scientist and iconic figure. His impact on developmental biology was immense, and his lasting legacy will include future discoveries of his many trainees. He lives on in the fond memories of his colleagues, family, and friends.