

OBITUARY

Edward B Lewis (1918–2004)

Prof. E. B. Lewis passed away on the 21st of July 2004 and with that ended an era in *Drosophila* genetics and developmental biology.

Transformation of the common fruitfly *Drosophila* to 'queen of genetics' took place in the beginning of 20th century in the 'flyroom' (Laboratory of Zoology, Columbia University, USA) of Thomas Hunt Morgan, the father of *Drosophila* genetics. For the first 40 years, the fruit fly was used as a means to study the mechanisms of inheritance. In 1950s, Ed Lewis played a very important role in the history of *Drosophila* by demonstrating the use of *Drosophila* to understand how genes program development. It is now one of the most studied organisms in developmental biology. Deservingly, Ed Lewis was appointed in 1966 as Thomas Hunt Morgan Professor of Biology (in Caltech, USA).

Ed Lewis spent his life working on the genetics of *Drosophila* with special attention to the genetic control of development. He worked on homeotic mutations, particularly *bithorax* mutations, in which organs that control balance (the halteres) were transformed to an extra pair of wings. Ed Lewis discovered that the extra pair of wings was due to transformation of the entire third thoracic segment to the second thoracic segment. He also studied several other types of homeotic transformations, for example, the first abdominal segment of *infra-abdominal* flies has a pair of legs, which are normally found only in thoracic segments. Ed Lewis further showed that homeotic transformations are due to single gene mutations, for example, inactivity of *Ultrabithorax* caused respecification of the 3rd thoracic segment into one that forms wings instead of halteres and, thereby, demonstrating that genes program development. Interestingly, homeotic genes are clustered on the chromosome as gene complexes. Ed Lewis showed that genes located proximally to the centromere on the chromosome control anterior body

segments while genes further down the genetic map controlled more posterior body segments (the colinearity principle). In 1978, he summarized his results in a review article (*Nature* 276, 565–570) and formulated theories about how homeotic genes interact, how the gene order corresponded to the segment order along the body axis, and how the individual genes are expressed. All of Ed Lewis's discoveries were purely based on genetic studies without much knowledge of the molecular nature of homeotic genes and what they code for. Later, it was discovered that homeotic genes code for DNA binding-transcription factors. They are highly conserved: from *Drosophila* to human (in vertebrates they are known as Hox genes). To an extent that human Hox genes can rescue, albeit partially, some of the homeotic mutations in *Drosophila*. The colinearity of homeotic gene complexes is also conserved between *Drosophila* and vertebrates. His pioneering work on homeotic genes induced other scientists to examine genetic control of all aspects of development. In 1995, Ed Lewis was awarded Nobel Prize in Physiology or Medicine for his work on *bithorax* complex.

Ed Lewis was a unique individual who worked at the bench throughout his career. In addition to working on *bithorax* complex genes and demonstrating their regulatory role in specifying segment-specific pathways, several fly stocks that all drosophilists use everyday (such as balancers, deficiency stocks, hundreds of other mutant stocks) were generated by him. He worked quietly to map all the deletions, inversions, etc. for decades. Ed Lewis is mainly responsible for spreading T.H. Morgan's concept of free exchange of ideas, sharing fly stocks and other reagents. He was the binding force for all drosophilists who have formed a close and cooperative family within the larger scientific community.

The best tribute we could offer to Ed Lewis is by adhering to his principles: free exchange of ideas, stocks and reagents. Every time we push a fly, use a balancer stock or a deficiency line, we remember Ed Lewis.

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