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# Transposable Elements

Edited by H. Saedler and A. Gierl

With 42 Figures



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*Cover illustration: The phenomenon of variegation in plants has always attracted scientists and artists. The latter is evident from the Japanese wood block prints collected by Lord Yoritaka Matsudaira (1711–1772). Shaseiga-chou represents a collection of Japanese morning glory (Asagao) phenotypes, an old medicinal plant, including variegated flowers. The insert shows a photograph kindly provided by Professor Shigeru Iida, Science University of Tokyo, exhibiting somatic excisions of the Tpn1 element from Japanese morning glory (see p. 155, this volume). (The wood block print is reprinted here with kind permission of Yoritaka Matsudaira, The Matsudaira Foundation.)*

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## Preface

Most genes are lined up on chromosomes like pearls on a string. However, a certain class of genes differ by being highly mobile; they are termed transposons. Their properties and the mechanism of transposition will be described in this book.

Where uniformity is the rule, irregularities like a spot on a plain-coloured surface strike the eye. Thus the phenomenon of variegation among organisms has long been a source of fascination. In plants, variegation is most easily recognised as irregularities in pigment patterns on leaves, flowers and seeds, but other characteristics such as leaf or flower form might also show variegation. In 1588, such a variegation pattern was described in kernels of *Zea mays* by Jacob Theodor of Bergzabern, a village south of Strasbourg. The report by Theodor is so detailed that if one counts the different kernel phenotypes described it becomes clear that the author is looking at a Mendelian segregation. It goes without saying that Latin-American Indians had already bred such variegated material much earlier, but no descriptions have yet been uncovered. Meanwhile, genetically heritable variegation patterns have been described at many different loci in more than 34 different plant species.

In the late 1940s, Barbara McClintock developed the concept of what she termed "controlling elements" based on variegation patterns. These "controlling elements" were genetic units associated with a gene, for example one involved in kernel pigmentation of *Zea mays*, thus controlling the expression of that gene. This would result in colourless kernels which feature many coloured spots due to the instability of the element, a phenotype already described by Jacob Theodor in 1588. Through her very thorough genetic analysis, for which McClintock received the Nobel prize in 1983, the current picture of transposable elements ultimately evolved.

The concept is that transposable elements are genetic entities which can migrate through the genome of an organism. However, a molecular understanding of this simple picture required a long journey from early genetic to current molecular

studies, which involved many diverse organisms and laboratories. In the mid 1960s, revertible polar mutations in the galactose operon of *Escherichia coli* were under study in Cologne and elsewhere. In 1968 these were shown to be due to DNA insertion (IS) elements. Their relationship to "controlling elements" in corn soon became apparent. At about that time a mutation of the white locus of *Drosophila melanogaster* was described, which had similar properties to an IS1 mutation in the gal operon of *E. coli*, i.e., both induced chromosomal deletions flanking the mutation. However, it was not until 1973, when heteroduplex studies with F and R DNA revealed the presence of IS elements on these plasmids, that a larger group of scientists became interested in DNA insertion elements, thus merging the field of medical bacteriology with molecular studies of DNA insertion elements. It soon became clear that IS elements could border other genes, in particular antibiotic resistance genes, and cause them to transpose from one DNA molecule to another. Subsequently it was found that many antibiotic resistance genes were organized in such structures, thereby allowing transposition.

In the 1980s, the field expanded further due to the isolation of plant transposable elements. Molecular studies revealed that McClintock's "controlling elements" were indeed DNA insertion elements. The analysis of their structure and function prevailed throughout the 1980s and the early 1990s. While in the bacterial and fly worlds researchers had moved to the analysis of the mechanism of transposition, in the plant world emphasis was placed on the use of these elements as tools to isolate other genes of interest. Transposon tagging soon became a powerful technique to isolate fly and plant genes even in heterologous hosts.

Although our knowledge about transposons in various organisms such as bacteria, flies and plants is ever increasing, their biological relevance remains obscure. In the current volume the state of research on transposons in various organisms is reviewed, in the hope of attracting researchers from other fields to enjoy and hopefully contribute to this fascinating field of science.

Köln

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