Evolution of transposable elements and evolution of eukaryote genomes mediated by transposable elements

Hiddenori Nishihara

School of Life Science and Technology, Tokyo Institute of Technology, Yokohama, Kanagawa 226-8501, Japan

Given the high rate at which eukaryotic genomes are being sequenced, it is no exaggeration to say that a full understanding of any particular genome is impossible without a deep characterization and analysis of transposable elements (TEs). TEs occupy from a small to a large proportion of eukaryotic genomes, e.g., 48% of the human genome and 85% of the maize genome. TEs are sometimes simply regarded as ‘repeats’, but they are actually highly diverse and have been classified into defined hierarchical groups according to transposition type, domain structure and sequence. In addition, TEs themselves evolve, and certain TE families can arise *de novo* and subsequently mobilize within the genome during evolution. Despite the large number of eukaryotic TE families that have been characterized recently, there are almost certainly a vast number of TEs in eukaryotes that remain to be identified.

TEs are often thought of as genomic parasites or selfish DNA. However, given the very large numbers of TEs present in eukaryotic genomes, it is unlikely that they have only neutral or negative effects on the host genome, and some of them are expected to have a positive effect(s) on genomic function and indeed may promote the evolution of the host species. Nearly half a century ago, Roy Britten and Eric Davidson proposed a far-sighted model for gene regulatory systems into which a subset of repetitive elements were incorporated. Over the subsequent decades, many studies have demonstrated the interrelationship between TEs and host organisms. Namely, TEs maximize their survival via transposition in the host genome. On the other hand, host species mostly repress the transposition of TEs but sometimes utilize them as functional elements (exaptation or co-option). A variety of TEs have been reported to have essential or assistive effects on various cellular processes such as gene regulation, cell fate and development, which supports the

Britten–Davidson model. Utilization of more TEs as functional sequences—such as novel genes or regulatory elements—might have allowed host cells to acquire more robustness and/or flexibility of genome regulation, which might confer evolutionary benefits on the host organism.

These properties of TEs imply that a thorough analysis of a eukaryotic genome from the viewpoint of TEs could lead to a discovery of their deep involvement in various cellular functions. Because the wide variety of TEs may have broad effects on cellular and genomic functions, it has become increasingly important that knowledge about TEs be shared among not only TE researchers but also the wide range of scientists who study genomics and genome evolution.

In this issue of *Genes & Genetic Systems*, three review articles outline our current understanding of the evolution of TEs and discuss their impact on the evolution of the host genome from various perspectives. First, Kenji Kojima summarizes our knowledge concerning the diversity of TE sequences and structures in eukaryotic genomes and presents a standardized, comprehensive classification scheme for TEs that has been developed in Repbase. Second, Masayuki Horie presents several examples of biological functions of riboviral sequences in the host and discusses tripartite interactions among eukaryotes, retrotransposons and riboviruses during evolution. Finally, I discuss the observation that host genome diversity is generally increased by the presence of TEs. I also summarize the functions of exapted TEs in mammals and postulate that TEs may have had a greater impact on genome function in a wider variety of animals than previously thought. These reviews bring together cutting-edge trends in TE research and provide essential perspectives for future studies toward the goal of fully understanding the long-term coexistence and evolution of TEs and eukaryotes.