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# Functional Adaptations to their Host Underlie the Evolutionary Diversification of Endogenous Retroviruses

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## Abstract

Transposable elements profoundly affect the biology and evolution of their hosts, yet their own evolutionary dynamics remain poorly understood. Here, we investigate insect endogenous retroviruses (iERVs), a monophyletic group of LTR retrotransposons that have acquired the trait of infectivity, likely through capture of a Baculovirus *envelope* gene. In *Drosophila* ovaries, iERVs with functional *envelope* have adapted their expression to any somatic cell type, from where they infect the germline. Strikingly, related retroviruses show distinct expression patterns, indicating niche partitioning. In contrast, all non-infectious iERVs that emerged through secondary *envelope*-loss are specifically expressed in the germline. Using transgenic reporters *in vivo* and sequence analysis of multiple iERV lineages including the variants of the transition element *rover*, we elucidate how this discrete co-variation evolved via changes in *i*) the elements transcriptional *cis*-regulatory sequences and *ii*) their functional envelope status (intact/defective). Notably, **the genome-protecting piRNA pathway - co-evolving with iERVs - has assimilated iERV promoter and sequence information into piRNA clusters, underscoring the functional significance of iERV expression in somatic niches. We propose that the evolutionary innovation of cell-to-cell infectivity gave rise to the iERV ancestor which then diversified through trait diversification and antagonistic virus-host interactions, processes that likely underpin niche-specific expression of endogenous retroviruses in vertebrates as well.**

**Keywords:** gypsy, *Drosophila*, evolution, envelope, infectivity

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