

Review

# Emerging Opportunities to Study Mobile Element Insertions and Their Source Elements in an Expanding Universe of Sequenced Human Genomes

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**Abstract:** Three mobile element classes, namely *Alu*, LINE-1 (L1), and SVA elements, remain actively mobile in human genomes and continue to produce new mobile element insertions (MEIs). Historically, MEIs have been discovered and studied using several methods, including: (1) Southern blots, (2) PCR (including PCR display), and (3) the detection of MEI copies from young subfamilies. We are now entering a new phase of MEI discovery where these methods are being replaced by whole genome sequencing and bioinformatics analysis to discover novel MEIs. We expect that the universe of sequenced human genomes will continue to expand rapidly over the next several years, both with short-read and long-read technologies. These resources will provide unprecedented opportunities to discover MEIs and study their impact on human traits and diseases. They also will allow the MEI community to discover and study the source elements that produce these new MEIs, which will facilitate our ability to study source element regulation in various tissue contexts and disease states. This, in turn, will allow us to better understand MEI mutagenesis in humans and the impact of this mutagenesis on human biology.

**Keywords:** *Alu*; LINE-1; L1; SVA; mobile element insertions; human genomes



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## 1. Introduction

Mobile genetic elements occupy approximately half of the human genome [1]. However, only three element classes, i.e., *Alu*, LINE-1 (L1), and SVA elements, remain actively mobile and continue to mutagenize human genomes today [2–15]. All three of these element classes are non-LTR retrotransposons that are mobilized through RNA intermediates using the protein machinery that is encoded by the L1 retrotransposon. Specifically, the L1-encoded proteins ORF1p and ORF2p generate new *Alu*, L1, and SVA “offspring” mobile element insertions (MEIs) through a mechanism that is termed target primed reverse transcription (TPRT) [16] (Figure 1). ORF1p encodes a nucleic acid chaperone [17,18], whereas ORF2p encodes an endonuclease (EN) [17,19] and a reverse transcriptase (RT) [17,20]. Since the L1 machinery mobilizes all three of these element classes [17,21–23], new *Alu*, L1, and SVA MEIs share characteristic features of L1 elements, including L1-like target site duplications (TSDs), poly (A) tails, and interior mutations that may be created by the error-prone L1 reverse transcriptase.

New MEIs are generated both in the germline [6–15] and in at least some somatic human tissues (i.e., epithelial cancers [6,24–30], reviewed in [31,32] and neuronal tissues [33–38], reviewed in [39]). Germline MEIs have been implicated in several dozen human diseases, including hemophilia [40], neurofibromatosis [41], and Duchenne muscular dystrophy [42] (reviewed in [43,44]). Somatic MEIs have been implicated in a wide range of epithelial cancers, including colon, lung, liver, esophageal, and pancreatic cancer (reviewed in [31,32]) and in several neurological diseases, including Rett Syndrome, Aicardi-Goutieres Syndrome, Schizophrenia, Amyotrophic Lateral Sclerosis (ALS), and normal aging (reviewed

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