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The Hidden Mutational Landscape of Extrachromosomal Circular DNA

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Abstract

The human genome is not confined to chromosomes. Extrachromosomal circular DNA—eccDNA and its megabase-scale counterpart ecDNA—is a persistent, transcriptionally active, and mutationally accelerated compartment present in normal and neoplastic cells. Yet every stage of genomic analysis, from DNA extraction to variant annotation, is engineered for linear, diploid templates. This review argues that circular DNA mutations are not rare events; they are systematically erased by methodologies that mistake the map for the territory. We synthesize evidence that circular DNA exhibits a mutational spectrum fundamentally distinct from chromosomal DNA: microhomology-driven indels, complex structural rearrangements within single molecules, and interchromosomal chimeric fusions that generate novel oncogenic reading frames. Its mutation rate is accelerated by rolling-circle replication, suppressed homologous recombination, and torsional stress—quantified as $\mu_{eff} = \mu_{bp} \times CN \times f_{rep}$, exceeding chromosomal rates by two orders of magnitude. Experimental isolation and detection methods each carry specific biases that distort mutational discovery. Computational reconstruction requires graph-based assembly and copy-number-normalized burden metrics. Validation by inverse PCR, mutation-specific FISH, and single-cell sequencing reveals that ecDNA mutations exhibit non-Mendelian inheritance yet drive transient transcriptional dominance. Major barriers include the absence of a circular reference genome, indistinguishable replication errors, and zero clinical standardization. Nevertheless, ecDNA amplifications occur in 14% of cancers, confer prognosis independent of chromosomal status, and serve as privileged sites for resistance mutations. eccDNA burden tracks cellular age and genotoxic stress. Emerging therapies targeting ecDNA segregation or transcription are plausible but lack specificity. The central conclusion is not that circular DNA matters—it is that the genome is not what we thought it was.

Keywords: Extrachromosomal Circular DNA, ecDNA, eccDNA, Somatic Mutations, Genomic Instability, Cancer Evolution, Therapeutic Resistance.

The Chromosome-Centric Fallacy

Genomics operates on an unexamined premise: that the genome and the chromosome complement are synonymous. This premise, inherited from classical genetics and enshrined in reference assemblies, has rendered an entire genetic universe invisible.

Extrachromosomal circular DNA is not an occasional aberration. It is a constitutive feature of eukaryotic genomes, present in healthy somatic tissue, emerging during cellular aging, and explosively amplified in malignancy (Møller et al., 2018; Paulsen et al., 2019). Unlike linear chromosomes, circular DNA lacks telomeres, replicates via rolling-circle mechanisms unconstrained by once-per-cycle licensing, and segregates randomly at mitosis. These are not minor topological variations. They are fundamental differences in genetic behavior that demand corresponding differences in how we detect, quantify, and interpret mutations.

Current practice does the opposite. Standard workflows are each optimized against circular DNA. The result is not merely underdetection but systematic erasure.

A Distinct Mutational Regime

Circular DNA does not mutate faster simply because it replicates more often. It mutates differently.

Single Nucleotide Variants. SNVs arise preferentially at microhomology tracts flanking double-strand breaks repaired by microhomology-mediated end joining, enriching C>A and T>C transitions (Carvalho & Lupski, 2016). Because ecDNA replicates under a random-copy-number model—multiple initiation events per cell cycle—a single polymerase error can generate hundreds of mutant copies within one division.

Insertions And Deletions. Indels are disproportionately frequent. Circular replication origins are singular; stalled forks cannot be rescued by adjacent origins. Template switching, the dominant rescue mechanism, skips intervening sequence, producing deletions of ±1 to ±50 bp at rates exceeding chromosomal DNA by several-fold (Shoshani et al., 2021). Serial switching can also generate insertions and tandem duplications. Aged fibroblasts accumulate eccDNA indels linearly with replicative age (Møller et al., 2018).

Structural Rearrangements. Rolling-circle replication drives intra-molecular recombination, producing head-to-tail concatemers that triplicate oncogenic segments within single circles (Purshouse et al., 2022). Inversions occur via intra-molecular polymerase direction switches. Secondary deletions within circles can remove co-extruded tumor suppressors (Koche et al., 2020).

Chimeric Sequences. Single eccDNA molecules frequently fuse fragments from two to four chromosomes via non-homologous end joining—localized chromoplexy condensed into extrachromosomal particles (Wu et al., 2019). These chimeras create neo-antigens and oncogenic fusions invisible to standard structural variant callers.

Epimutations. Large ecDNA (>1 Mb) is densely chromatinized. Circles exhibit loss of maintenance methylation and ectopic enhancer adoption, creating heritable expression changes without sequence alteration (Hung et al., 2021).

Quantitative Acceleration. The effective mutation rate for an ecDNA-encoded oncogene is:

$\mu_{eff} = \mu_{bp} \times CN_{avg} \times f_{rep}$

where $f_{rep} \approx 3–5$. At $CN_{avg} = 50$, μ_{eff} exceeds chromosomal rates by two orders of magnitude (Luebeck et al., 2023).

Methodological Blind Spots

Enzymatic Selection. Exonuclease V and T digestion enriches circular DNA 10^3–10^4-fold but introduces survivor bias: nicked circles—those actively repairing or mutation-prone—are linearized and degraded (Shibata et al., 2012; Kumar et al., 2017).

Rolling Circle Amplification. Phi29 polymerase provides 10,000-fold selectivity but lacks proofreading. Error rate: 1×10^{-5}–10^{-6} per base per pass. A 1,000-fold amplification yields ~1 error/kb, indistinguishable from authentic mutations (Dean et al., 2001; Lou et al., 2013). Small circles amplify preferentially.

Density Separation. CsCl-ethidium bromide gradients preserve native distribution but require microgram inputs and fragment large ecDNA (Radloff et al., 1967; Johnson & Grossman, 1977).

Circle-Seq. Junction-spanning reads identify circular breakpoints but lose physical linkage between distal SNVs on the same molecule. Rare circles (<1 copy/100 cells) fall below detection (Møller et al., 2016; Zhao et al., 2022).

Long-Read Sequencing. PacBio HiFi and Nanopore ultra-long reads resolve entire ecDNA molecules, including complex structural variants and methylation patterns. Raw error rates remain prohibitive for SNV calling without circular consensus or hybrid correction (Huddleston et al., 2017; Wenger et al., 2019; Simpson et al., 2017).

CRISPR Capture. dCas9 affinity pull-down achieves >1,000-fold enrichment of known circular loci, detecting variants below 0.1% frequency. Requires a priori sequence knowledge (Sipos et al., 2019; Zhang et al., 2021).

Computational Reconstruction

Graph-Based Assembly. Circular molecules form closed cycles in De Bruijn graphs—strongly connected components without free ends. Dedicated assemblers (Circle_finder, CIDER-seq) identify these cycles (Bankevich et al., 2012; Ghareghani et al., 2022).

Junction-Aware Calling. Standard callers misclassify junction-spanning mismatches as SNVs. Circle-Map and eccDNA_VariantCaller perform local realignment around junctions, suppressing false positives (Prada-Luengo et al., 2019).

Copy-Number-Normalized Burden. Conventional TMB assumes diploidy. For ecDNA, we propose:

$$CNMB = (\Sigma\ VAF_i \times CN_{ecDNA}) / L_{ecDNA}$$

This reports mutations per individual circular molecule. CN_{ecDNA} is inferred by AmpliconArchitect or ecSeg from junction-spanning read density (Deshpande et al., 2019; Luebeck et al., 2020).

Experimental Validation

Inverse PCR. Outward-facing primers amplify only circularized templates. Sanger sequencing across the junction validates breakpoints and adjacent SNVs at single-base resolution. Low-throughput; requires known junctions (Shibata et al., 2012; Møller et al., 2018).

Mutation-Specific FISH. LNA or PNA probes discriminate single-nucleotide mismatches under stringent hybridization. Reveals ecDNA hub clustering and spatial segregation of mutant alleles. Limited to large ecDNA (>500 kb) (Turner et al., 2017; Hung et al., 2021).

Single-Cell Sequencing. scCircle-seq achieves eccDNA detection in >70% of cancer cells. EcDNA copy number follows Pareto distribution; minority 'ecDNA reservoirs' harbor hundreds of copies. Enables haplotype-resolved mutation phasing (Andor et al., 2020; Chamorro González et al., 2023; Luebeck et al., 2023).

Biological Consequences

Transient Mutational Dominance. ecDNA mutations segregate randomly at mitosis. A resistance-conferring mutation arising on a single ecDNA copy can amplify to population dominance within few generations—then contract upon drug withdrawal, leaving no trace in the chromosomal archive (Nathanson et al., 2014; deCarvalho et al., 2018).

Dual-Speed Genome. Chromosomes provide long-term evolutionary memory; circular DNA provides short-term adaptive plasticity. The two systems operate under different mutation rates, repair biases, and inheritance rules (Verhaak et al., 2019; Wu et al., 2019).

Barriers to Translation

No Reference Genome. Each eccDNA is a unique somatic fusion absent from GRCh38. Investigators choose between alignment to linear coordinates (misses internal mutations) or de novo assembly (introduces errors) (Dutta & Sengupta, 2022; Prada-Luengo et al., 2020; Zhao et al., 2021).

Artifact Discrimination. Amplification artifacts (phi29 errors), replication errors (in vivo rolling-circle mistakes), and junction misalignment are currently indistinguishable from authentic mutations.

No Clinical Standards. Protocols vary wildly across laboratories. No reference cell line with characterized ecDNA copy number, junctions, and mutation status exists. Clinical interpretation of ecDNA variants is absent (Haber & Schimke, 2021; Verhaak et al., 2019).

Future Directions

Diagnostic Integration. ecDNA-aware algorithms applied to existing tumor sequencing data can identify ecDNA amplifications, which occur in 14% of cancers and predict poor outcomes. Adaptation to CLIA standards is urgently needed (Kim et al., 2020; Luebeck et al., 2020).

Biomarker Development. eccDNA burden correlates with donor age and genotoxic stress. Pre-neoplastic eccDNA junctions are detectable years before malignant transformation in Barrett's esophagus and cirrhotic liver (Kumar et al., 2017; Luebeck et al., 2023).

Therapeutic Targeting. Four strategies are under investigation: ecDNA elimination (bromodomain inhibitors, DNA intercalators), segregation disruption, replication inhibition, and transcriptional interference (ecDNA hub disruption). Specificity remains the central unsolved problem (Wu et al., 2019; Hung et al., 2021).

Conclusion: The Mutation That Was Always There

A tumor biopsy is sequenced. The pipeline reports no actionable mutations. The patient progresses. Retrospective ecDNA-aware analysis identifies an EGFR C797S mutation on a highly amplified ecDNA molecule—present at diagnosis, invisible to linear genomics.

This is not hypothetical. It has happened, and continues to happen (deCarvalho et al., 2018). The mutation was not absent. It was not rare. It was not below the limit of detection. It was simply incompatible with the linear reference model.

Circles that mutate are not exceptions to genomic stability. They are the rule—the manifestation of a genome that is dynamic, adaptive, and not coextensive with its chromosomes. For decades, genomics has mapped the stars while the planets remained dark. It is time to turn the telescope toward the circular darkness. The mutations are not rare. They are waiting to be seen.

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