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Evolving together: Cassandra retrotransposons gradually mirror promoter mutations of the 5S rRNA genes

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The 5S rRNA genes are among the most conserved nucleotide sequences across all species. Similar to the 5S preservation we observe the occurrence of 5S-related non-autonomous retrotransposons, so-called Cassandra. Cassandras harbor highly conserved 5S rDNA-related sequences within their long terminal repeats (LTRs), advantageously providing them with the 5S internal promoter. However, the dynamics of Cassandra retrotransposon evolution in the context of 5S rRNA gene sequence information and structural arrangement are still unclear, especially: 1) do we observe repeated or gradual domestication of the highly conserved 5S promoter by Cassandras and 2) do changes in 5S organization such as in the linked 35S-5S rDNA arrangements impact Cassandra evolution? Here, we show evidence for gradual co-evolution of Cassandra sequences with their corresponding 5S rDNAs. To follow the impact of 5S rDNA variability on Cassandra TEs, we investigate the Asteraceae family where highly variable 5S rDNAs, including 5S promoter shifts and both linked and separated 35S-5S rDNA arrangements have been reported. Cassandras within the Asteraceae mirror 5S rDNA promoter mutations of their host genome, likely as an adaptation to the host's specific 5S transcription factors and hence compensating for evolutionary changes in the 5S rDNA sequence. Changes in the 5S rDNA sequence and in Cassandras seem uncorrelated with linked/separated rDNA arrangements. We place all these observations into the context of angiosperm 5S rDNA-Cassandra evolution, discuss Cassandra's origin hypotheses (single or multiple) and Cassandra's possible impact on rDNA and plant genome organization, giving new insights into the interplay of ribosomal genes and transposable elements.