PERSPECTIVE

An integrative model for the emergence and conservation of minor introns

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ABSTRACT

Since their discovery, minor introns, which make up around 0.5% of the introns in the human genome, have been a mystery. The minor spliceosome, a unique splicing complex, eliminates these introns. Both have a long evolutionary history that dates back to the Last Eukaryotic Common Ancestor (LECA), as seen by minor intron enrichment in particular gene families such as the voltage-gated sodium and calcium ion channels, mitogen-activated protein kinases, and E2F transcription factors. In genes with a preponderance of major introns, the majority of minor introns are found as single introns. This arrangement increases the likelihood of missplicing since Minor Intron-Containing Gene (MIG) expression necessitates the coordinated action of two spliceosomes. Therefore, one would anticipate modest intron loss through purifying selection. At least nine eukaryotic lineages have experienced complete minor intron loss as a result of this. The importance of minor introns is highlighted by the embryonic lethality that results from the inactivation of the minor spliceosome in land plants and metazoans, where they are highly conserved. Rapidly proliferating progenitor cells are extremely vulnerable to minor spliceosome loss, as demonstrated by conditional inactivation of the minor spliceosome. In fact, we discovered that MIGs were considerably enriched in a 341 cycling cell line screen for genes necessary for survival. Here, we suggest that minor introns were randomly inserted into genes in LECA or earlier and were later conserved in genes essential for cycling cell viability. We propose that minor introns survived the unicellularity of early eukaryotic evolution because of the essentiality of MIGs. Further supporting our essentiality paradigm for MIG conservation, we found 59 MIGs that appeared after LECA, several of which are crucial for cycling cell survival. This shows that the development of minor introns is dynamic throughout the evolution of eukaryotes and that minor introns should not be thought of as molecular fossils. We further suggest that minor intron splicing was used as a regulatory switch for en masse control of MIG expression and the biological processes it regulates during multicellular evolution. According to domestication syndrome, which shows that MIGs are enriched in common candidate genes for animal domestication, this mode of regulation could specifically control cell proliferation and consequently body size.

Key Words: *Proliferation; Mitogen-activated; Domestication; Embryonic; Intron containing; Minor Spliceosome*

INTRODUCTION

The majority of eukaryotic protein-coding genes require the removal of non-coding intronic regions from their pre-mRNA transcripts and the ligation of their coding exons in order to be expressed. Major introns, which make up more than 99.5% of introns in many eukaryotes, and minor introns, which make up less than 0.5% of introns, are the two different types of introns. Two distinct splicing machines must recognise and remove these introns due to the differences in consensus sequences of the major and minor introns. These splicing apparatuses are spliceosomes, which are ribonucleoprotein complexes that comprise five Short Nuclear RNAs (snRNAs) and a number of related proteins. Only the major spliceosome, which is made up of the snRNAs U1, U2, U4, U5, and U6, is capable of removing large introns. The minor spliceosome, which is made up of the shared U5 snRNA and the unique snRNAs U11, U12, U4atac, and U6atac, excises minor introns. The origin of major and minor introns, as well as their corresponding spliceosomes, is thought to have occurred at or before the Last Eukaryotic Common Ancestor (LECA).

Minor Intron-Containing Genes (MIGs) have only one or two minor introns and a majority of major introns. Therefore, in order to generate MIGs, both spliceosomes must be expressed, formed, and

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recruited. Additionally, there must be spatiotemporal coordination between major and minor spliceosome activity along the pre-mRNA transcript. Because both spliceosomes use the same transcription and processing pathways, the expression and production of two distinct spliceosomes raise the metabolic burden on the cell. For instance, RNA polymerase II and RNA polymerase III activity are required for the expression of all spliceosomal snRNAs. Then, by using common pathways, these developing snRNAs must be transformed into their mature versions. The U5 snRNA and more than 30 proteins that are shared by the minor and major spliceosomes are also necessary for the development of the minor spliceosome. Therefore, to maintain regular rates of gene expression and major spliceosome assembly, the expression and assembly of the minor spliceosome require increased production of several nuclear, nuclear envelope-bound, and cytoplasmic proteins. One would expect strong purifying selection against minor introns and the minor spliceosome given the intricate spliceosomal coordination necessary for MIG expression and the substantial metabolic load associated with the maintenance of the minor spliceosome. In particular, since minor introns and the minor spliceosome emerged in early, unicellular eukaryotes, effective population size is positively correlated with the strength of purifying selection, and unicellular species typically have high effective population sizes, one would anticipate that minor introns would have completely disappeared during early eukaryotic evolution. Minor introns and the minor spliceosome are present in many current genomes, demonstrating that they survived in numerous lineages, despite the fact that nine distinct occurrences of full loss of minor introns and the minor spliceosome have been found throughout eukaryotic evolution.

Particularly, the minor spliceosomes and minor introns are very conserved in metazoans and terrestrial plants. In fact, the positions of minor introns are more highly conserved in terrestrial plants and animals than the positions of big introns.