

Transposable elements and polyploid evolution in animals

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Polyploidy in animals is much less common than in plants, where it is thought to be pervasive in all higher plant lineages. Recent studies have highlighted the impact of polyploidization and the associated process of diploidy restoration on the evolution and speciation of selected taxonomic groups in the animal kingdom: from vertebrates represented by salmonid fishes and African clawed frogs to invertebrates represented by parasitic root-knot nematodes and bdelloid rotifers. In this review, we focus on the unique and diverse roles that transposable elements may play in these processes, from marking and diversifying subgenome-specific chromosome sets before hybridization, to influencing genome restructuring during rediploidization, to affecting subgenome-specific regulatory evolution, and occasionally providing opportunities for domestication and gene amplification to restore and improve functionality. There is still much to be learned from the future comparative genomic studies of chromosome-sized and haplotype-aware assemblies, and from postgenomic studies elucidating genetic and epigenetic regulatory phenomena across short and long evolutionary distances in the metazoan tree of life.

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Introduction

Polyploidy in animals has long been thought to be quite rare [1,2], in contrast to plant polyploidy, which is now recognized as being present in almost all lineages of higher plants [3,4]. Most of the polyploidization events investigated in the animal kingdom were initially focused on the more easily discernible paleopolyploidy, noted in several rounds of whole-genome duplications (WGD) at the base of vertebrate evolution [5], rather than

neopolyploidy, which is much harder to disentangle experimentally and bioinformatically. In recent years, we have witnessed much progress in genome sequencing technologies, which fortunately shows no signs of slowing down. With genome size and complexity no longer being the limiting factor, comparative genomics has finally drifted away from sequencing the genomes of haploids or highly inbred diploids. It is now rapidly moving towards resolving haplotypes in heterozygous diploids and towards analyzing complex genomes with several sets of chromosomes co-inhabiting the nuclei of polyploid plants and animals, including recent polyploids.

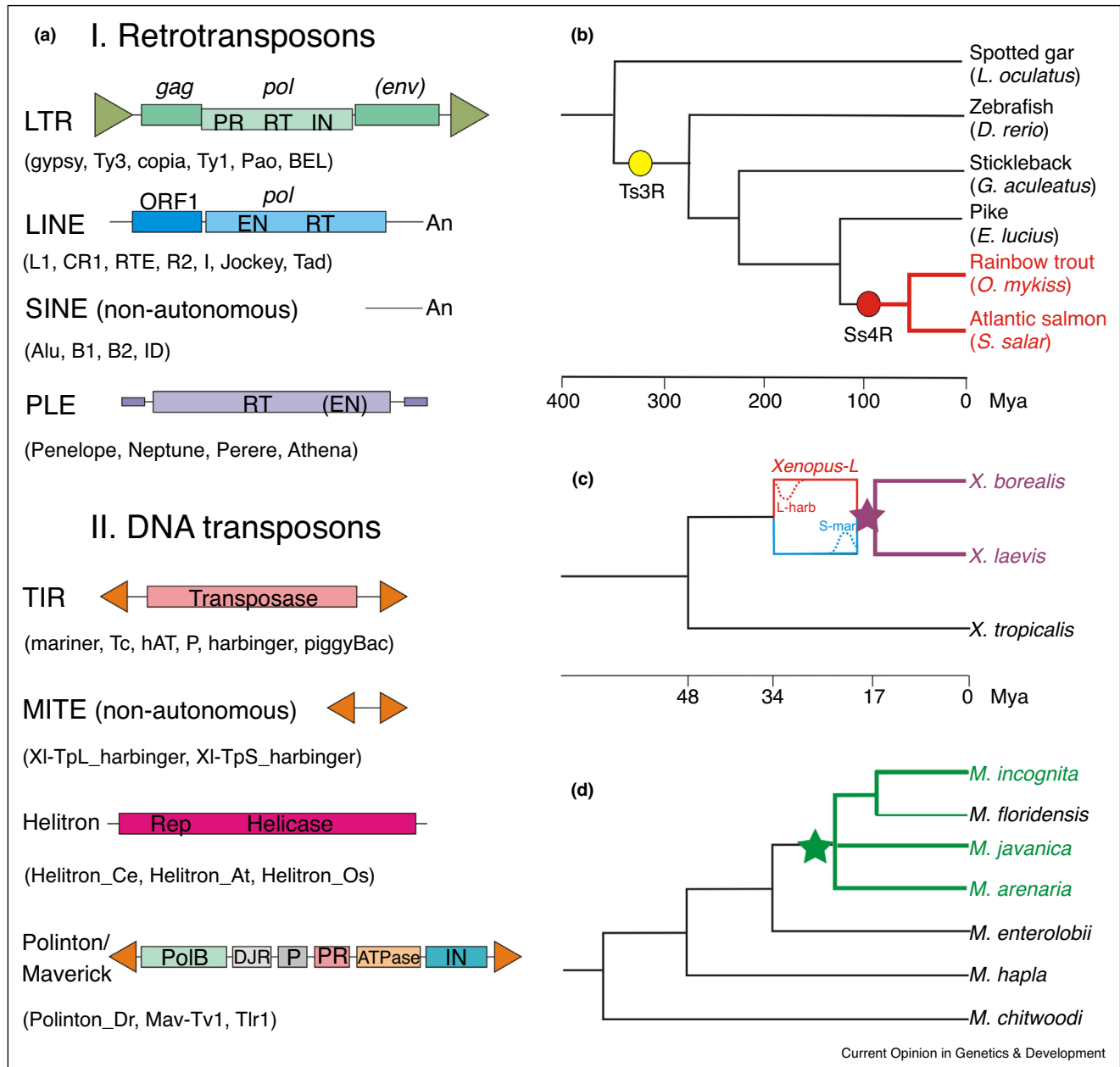
While ploidy changes can account, to a certain extent, for the huge variation in genome size that can be observed between different species, another major contribution to such variation is often provided by the expansion and contraction of the so-called ‘fluid component’ of eukaryotic genomes [6], which is represented largely by various types of transposable elements (TEs) (Figure 1a). Furthermore, the interplay of these two major contributing factors can result not simply in an increase or decrease in the genome size, but can bring about more profound genetic and epigenetic changes that could further define the evolutionary trajectories of individual species and larger taxonomic groups.

With several recent reviews summarizing the impact of TE proliferation and cyclical ploidy changes on the evolution of genome architecture in plants, both on the genetic and the epigenetic side [7–11], the timing is right to revisit the subject of TE-associated genetic and epigenetic changes in hybrid and polyploid animals, which we reviewed a few years ago [12], focusing specifically on those polyploid genomes for which TE analysis has been performed. The recently sequenced genomes of polyploid animals, from vertebrates such as fish and amphibians, to invertebrates including ecdysozoan and lophotrochozoan taxa, reveal some interesting parallels with plant genomes, but also suggest certain differences related to the less frequent occurrence of polyploidy in animals.

Fishes: transposons and rediploidization in salmonids

Vertebrate genomes were initially shaped by two rounds of ancient WGD events, which in fishes were followed by a teleost-specific round of WGD (Ts3R, also called TGD for teleost genome duplication), and additionally by a salmonid-specific round (Ss4R) [13] (Figure 1). For this

Figure 1



Transposable elements and representative species discussed in the text. **(a)** A compilation of major structural features for class I TE (retrotransposons) and class II TE (DNA transposons). Shown are the characteristic ORFs with functional domains (RT, reverse transcriptase; IN, integrase; PR, protease; EN, endonuclease; PolB, family B DNA polymerase; DJR, double jelly-roll capsid-like protein; P, penton protein) and direct or inverted repeats or poly-A stretches at the termini. Selected representatives, including those mentioned in the text and figures, are listed in parentheses. Not to scale. **(b)** Phylogenetic relationships in teleost fish and the ancestral spotted gar, with salmonids shown in red (after Ref. [15**]). Yellow and red circles represent the teleost-specific whole genome duplication (Ts3R) and the salmonid-specific whole genome duplication (Ss4R), respectively. **(c)** Phylogeny of *Xenopus* frogs according to [22**]. Hybridization between the progenitor *Xenopus*-L and *Xenopus*-S species is denoted by purple star. Estimated peaks of L-harbinger and S-mariner activity are shown at 33–34 Mya and 18 Mya, respectively. **(d)** A consensus phylogram illustrating relationships between root-knot nematodes discussed in the text, based on [24*, 25, 26*]. Species with elevated ploidy are shown in green; the green star denotes the presumed recent hybridization(s), the precise time estimate for which was not reported. *M. javanica* is shown as a polytomy, since its phylogenetic placement differs in [24*, 26*]. In (b–d), the cases of ploidy increase are shown by colored lines with double thickness.

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