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Expansion of a single transposable element family is associated with genome-size increase and radiation in the genus Hydra

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Transposable elements are one of the major contributors to genome-size differences in metazoans. Despite this, relatively little is known about the evolutionary patterns of element expansions and the element families involved. Here we report a broad genomic sampling within the genus Hydra, a fresh-water cnidarian at the focal point of diverse research in regeneration, symbiosis, biogeography, and aging. We find that the genome of Hydra is the result of an expansion event involving long interspersed nuclear elements and in particular a single family of the repeat element 1 (CR1) class. This expansion is unique to a subgroup of the genus Hydra, the brown hydridas, and is absent in the green hydra, which has a repeat landscape similar to that of other cnidarians. These features of the genome make Hydra attractive for studies of transpon-driven genome expansions and speciation.

Using transcriptome data, we searched for evidence of a genome duplication event in the brown hydridas. We found that 75% (8,629 out of 11,543) of gene families had the same number of genes in both H. viridissima and H. vulgaris. Additionally, 84.7% and 81.1% of the gene families contained a single gene from H. vulgaris and H. viridissima, respectively. Thus, there was no evidence for genome duplication as the explanation for the large genome size in the brown hydridas. However, a good reference assembly for the green hydra genome will be required to completely rule out a rediploidization scenario.

To test the contribution of TEs to the Hydra genome expansion, we used DNAPipeTE (15) to identify and assemble highly abundant DNA reads from a random sample of 1 million reads from each species. We found that all of the major TE classes are represented at similar levels in the Hydra genomes with the exception of long interspersed nuclear elements (LINEs). LINEs were strikingly enriched (>6-fold) in the brown hydra genomes (Fig. 1B). We found that 2 of the 3 major LINE classes are over-represented, L2 and CR1 (16), comprising at least 8 to 12% of all sampled reads in brown hydridas compared to less than 0.5% in the green hydra.

To determine the evolutionary history of LINEs in the brown hydridas, we constructed a similarity graph based on BLASTN scores among all detected LINE consensus sequences. While we could identify contributions from all CR1/L2 families, we found that the expansion was largely limited to a specific region of the graph (Fig. 2). This indicates that the largest expansion happened in only one or a few highly related CR1 families (as defined by DNAPipeTE), together responsible for at least 28% of the expansion among the brown hydridas.

We next investigated whether the CR1 expansion happened independently in each brown hydra lineage or at the base of the brown hydra clade. Based on similarity graphs of CR1 families (Fig. 2), we found that more than half of all DNAPipeTE CR1 families (e.g., 85 out of 116 CR1 families in Hydra circumcincta and 60 out of 105 CR1 families in Hydra oligactis) could be traced independently in each brown hydra lineage or at the base of the brown hydra clade. Based on similarity graphs of CR1 families (Fig. 2), we found that more than half of all DNAPipeTE CR1 families (e.g., 85 out of 116 CR1 families in Hydra circumcincta and 60 out of 105 CR1 families in Hydra oligactis) could be traced independently in each brown hydra lineage or at the base of the brown hydra clade. Based on similarity graphs of CR1 families (Fig. 2), we found that more than half of all DNAPipeTE CR1 families (e.g., 85 out of 116 CR1 families in Hydra circumcincta and 60 out of 105 CR1 families in Hydra oligactis) could be traced independently in each brown hydra lineage or at the base of the brown hydra clade.
back to the last common brown hydra ancestor. Interestingly, the majority of CR1 sequences in the genomes apparently lack the ability to propagate autonomously, as they are relatively short (478 bp on average, estimated by RepeatCraft, ref. 17).

Taken together, our findings show that a single CR1 family dominated the CR1/L2 LINE expansion after the separation of the green and brown hydra lineages. Given the wide distribution of these elements across the genome, an alternative scenario of repetitive element excision events that happened only in the green hydra lineage seems unlikely. Moreover, the repeat content of the green hydra genome is similar to that of other cnidian lineages (3,4), in which expansion is due to a combination of various repeat element classes in each genome. Genome sizes are from refs. 25 and 26.

Fig. 1. Phylogeny of the genus Hydra. (A) RAxML phylogeny of Hydra and other metazoans. Dating estimates are provided for each node. (B) Branching pattern and divergence within the genus Hydra. Age estimates in black are from this study, those in blue are from ref. 7, and those in red are from refs. 14 and 24. Bar charts on the right indicate proportions of the major repeat element classes in each species. Genome sizes are from refs. 25 and 26.

Materials and Methods

Hydra cultures were maintained using standard methods (19). DNA and RNA extractions were done using Qiagen kits. Library preparation and Illumina sequencing were done using standard methods. Sequences have been deposited in the NCBI Sequence Read Archive entry for the project (PRJNA147713). Transcriptomes were assembled with Trinity (20), filtered with CD-hit (21), and the peptides predicted with Transdecoder (22). Orthologous groups were constructed using OrthoFinder (23). The full analysis pipeline is available from https://github.com/niccw/hydracompgen.

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