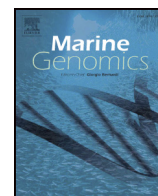




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## Marine Genomics



## Review

## Recent advances in genomics and transcriptomics of cnidarians

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## ARTICLE INFO

## Article history:

Received 14 July 2015

Received in revised form 20 September 2015

Accepted 21 September 2015

Available online xxxxx

## Keywords:

Cnidaria

Genome evolution

cis-Regulation

Transcriptome

Nematostella

Hydra

## ABSTRACT

The advent of the genomic era has provided important and surprising insights into the deduced genetic composition of the common ancestor of cnidarians and bilaterians. This has changed our view of how genomes of metazoans evolve and when crucial gene families arose and diverged in animal evolution. Sequencing of several cnidarian genomes showed that cnidarians share a great part of their gene repertoire as well as genome synteny with vertebrates, with less gene losses in the anthozoan cnidarian lineage than for example in ecdysozoans like *Drosophila melanogaster* or *Caenorhabditis elegans*. The *Hydra* genome on the other hand has evolved more rapidly indicated by more divergent sequences, more cases of gene losses and many taxonomically restricted genes. Cnidarian genomes also contain a rich repertoire of transcription factors, including those that in bilaterian model organisms regulate the development of key bilaterian traits such as mesoderm, nervous system development and bilaterality. The sea anemone *Nematostella vectensis*, and possibly cnidarians in general, does not only share its complex gene repertoire with bilaterians, but also the regulation of crucial developmental regulatory genes via distal enhancer elements. In addition, epigenetic modifications on DNA and chromatin are shared among eumetazoans. This suggests that most conserved genes present in our genomes today, as well as the mechanisms guiding their expression, evolved before the divergence of cnidarians and bilaterians about 600 Myr ago.

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## 1. The beginnings: cnidarians have a complex gene repertoire

It was as early as 1744 when Abraham Trembley, a Swiss physician, used the freshwater polyp *Hydra* to study regeneration and questions of tissue polarity (Trembley, 1744). Ever since, cnidarians, in particular the hydrozoan *Hydra* remained one of the prominent model systems in developmental biology. The versatile possibility to be manipulated on the cell and tissue level, for instance by transplantation and dissociation/reaggregation e.g. (Bode and Bode, 1980; Broun and Bode, 2002; Khalturin et al., 2009; Gierer et al., 1972; Technau and Holstein, 1992;

MacWilliams, 1983; Technau et al., 2000), as well as a virtually complete quantitative understanding of its cell composition and cell differentiation kinetics (Bode, 1996; Bode et al., 1990; David, 1973; David and Campbell, 1972; David and Gierer, 1974; Holstein and David, 1990; Holstein et al., 1991) (e.g. David and Murphy, 1977; Bosch and David, 1991) is a unique strength of this system and led to important insights in axis formation and cell differentiation of a simple organism. However, cnidarians are not readily amenable to genetics and therefore isolation of the first genes by low stringency screens and degenerate PCR had to rely on known sequences from other organisms. These attempts revealed that many of the key regulators of bilaterian development are present in Cnidaria and are often remarkably conserved in the crucial protein domains. Besides this homology-based candidate gene approach, others attempted to

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**Table 1**  
Genomic features of selected cnidarian and bilaterian model species.

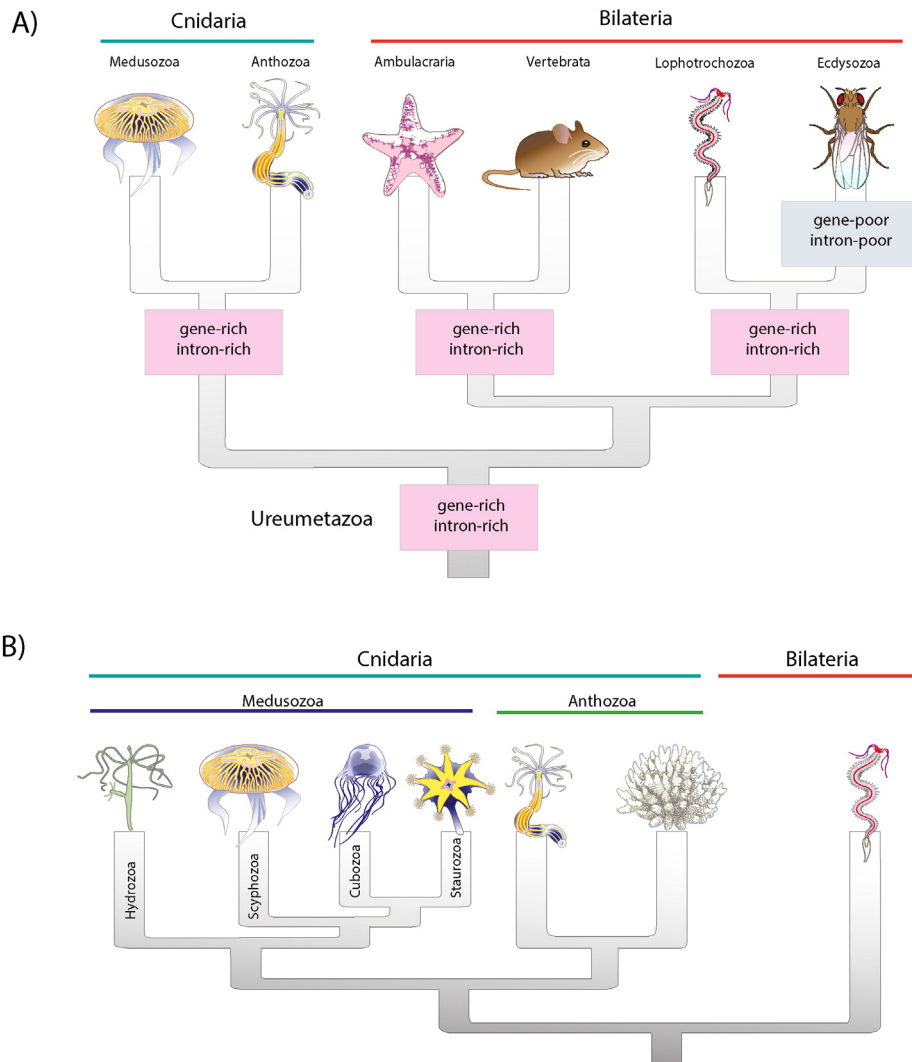
Species	Genome size	Gene models	Repetitive elements	Haploid chromosome number	N50 contigs	N50 scaffolds	Average gene length [bp]	Average size of intergenic region [bp]	Gene density (per 100 kb) <sup>a</sup>	AT content
<i>Nematostella vectensis</i>	450 Mbp	27,273 <sup>b</sup>	25%	15	19.8 kbp	472 kbp	6,517	4,981	8	59
<i>Acropora digitifera</i>	420 Mbp	23,700	13%	14	10.7 kbp	191.5 kbp	n.d.	n.d.	6.5	61
<i>Hydra magnipallilata</i>	1.0 Gbp <sup>c</sup>	20,000	57%	15	12.8/9.7 kbp <sup>c</sup>	63.4/92.5 kbp <sup>c</sup>	6,964	12,490	3.5	71
<i>Mus musculus</i>	2.6 Gbp	24,000	38%	20	n.d.	n.d.	41,760	65,850	1.5	58
<i>Drosophila melanogaster</i>	165 Mbp	16,000	3%	4	n.d.	n.d.	5,721	5,589	10	60

n.d. = not determined.

<sup>a</sup> The average gene density was calculated as number of predicted protein coding genes per genome size minus fraction of repetitive elements.<sup>b</sup> 27,273 gene models were predicted computationally by Putnam et al. (2007), of which 18,345 were considered as bona fide genes based on a re-evaluation using conservative criteria. See Putnam et al. (2007) for details.<sup>c</sup> The numbers correspond to the two existing complementary assemblies: CA and RP (Chapman et al., 2010).

identify head or cell type specific genes by differential library screens (Kurz et al., 1991; Weinzierl et al., 1994). However, because these approaches are laborious and tedious, the number of isolated and characterized genes remained small. The sequencing of Expressed Sequence Tag (EST) libraries allowed the identification of thousands of transcribed genes in a systematic and unbiased manner (Kortschak et al., 2003; Technau et al., 2005). The latter study united ESTs from two cnidarians,

the sea anemone *Nematostella vectensis* and the coral *Acropora millepora*, two anthozoans, which are separated by about 400–450 Myr. The intraphyletic and interphyletic comparison suggested a surprising degree of ancestral genetic complexity that was maintained in anthozoan cnidarians and several bilaterian lineages, e.g. the vertebrate lineage. Interestingly, about 8% of the Blast hits to Bilateria were exclusively shared with chordates, while about 1–2% were shared with ecdysozoan model species



**Fig. 1.** A) Phylogenetic tree of eumetazoans. We have indicated, for each branch of the tree, if the genome of the last common ancestor of this branch was gene/intron rich or poor, based on the sequenced genomes of representatives of this branch of the tree. Based on these observations, it is likely that the genome of the last common ancestor of all eumetazoans was gene rich and intron rich. B) Phylogenetic tree of Cnidarians (Collins et al., 2006). Representative Medusozoa depicted here are *Hydra viridis* (Hydrozoa), *Aurelia aurita* (Scyphozoa), *Chironex fleckeri* (Cubozoa) and *Haliclystus spec* (Staurozoa). The Anthozoa are the sea anemone *Nematostella vectensis* (left) and the coral *Acropora millepora* (right).

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