



Review article

Independent evolution of genomic characters during major metazoan transitions

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A B S T R A C T

Metazoan evolution encompasses a vast evolutionary time scale spanning over 600 million years. Our ability to infer ancestral metazoan characters, both morphological and functional, is limited by our understanding of the nature and evolutionary dynamics of the underlying regulatory networks. Increasing coverage of metazoan genomes enables us to identify the evolutionary changes of the relevant genomic characters such as the loss or gain of coding sequences, gene duplications, micro- and macro-synteny, and non-coding element evolution in different lineages. In this review we describe recent advances in our understanding of ancestral metazoan coding and non-coding features, as deduced from genomic comparisons. Some genomic changes such as innovations in gene and linkage content occur at different rates across metazoan clades, suggesting some level of independence among genomic characters. While their contribution to biological innovation remains largely unclear, we review recent literature about certain genomic changes that do correlate with changes to specific developmental pathways and metazoan innovations. In particular, we discuss the origins of the recently described pharyngeal cluster which is conserved across deuterostome genomes, and highlight different genomic features that have contributed to the evolution of this group. We also assess our current capacity to infer ancestral metazoan states from gene models and comparative genomics tools and elaborate on the future directions of metazoan comparative genomics relevant to evo-devo studies.

1. Introduction

Ancient animal evolution was shaped by several distinct and complex transitions of body-plan organization, most notably the origin of multicellularity (Ediacaran or Vendian) (Fedonkin, 2003; King, 2004; Narbonne, 2005; Richter and King, 2013; Stanley, 1973), followed by the emergence of bilaterally symmetric forms with a through-gut, and the centralized nervous system (Erwin et al., 2011; Knoll and Carroll, 1999). It is one major focus of evolutionary biology to understand those and other organismal transitions, at both the molecular-genetic and morphological levels. Over the past years, many studies have revealed a surprisingly high degree of shared gene complements (Degnan et al., 2009; Kortschak et al., 2003; Putnam et al., 2007; Wheeler et al., 2009) among the descendants of those ancient animals. Building on this shared genomic content, recent advances in evo-devo have contributed to our understanding of the function of those cascades in development across metazoans, revealing striking similarities (Carroll et al., 2013; Raff, 2000) of developmental programmes and transcriptional regulatory cascades as well as signaling pathway usage responsible for the patterning of the basic metazoan

body-plan (Degnan et al., 2009; Erwin, 2009).

Every new metazoan genome that was decoded revealed underlying genetic novelties at both coding and non-coding levels (Fig. 1). Such a tendency was found since the publication of the first metazoan genome, the nematode *C. elegans* (*C. elegans* Sequencing Consortium, 1998), revealing a striking number of gene duplications of olfactory receptors, relating to lineage-specific adaptation. The initial focus on the genomes of model organisms relevant to developmental biology or medical research, such as *Drosophila* or mouse, helped identify several patterns of metazoan evolution, contributing to the ongoing debates of the relative importance of different mechanisms contributing to organismal complexity, e.g., evolution through gene novelty and duplication (Kaessmann, 2010; Tautz and Domazet-Lošo, 2011) or regulation (Davidson and Erwin, 2006; Prud'homme et al., 2007).

Understanding the role of those processes during metazoan evolution requires the sampling of many phylogenetically informative species. With the help of the recent advances in sequencing technology, genomic studies were able to focus on species distributed over the whole metazoan tree of life (Fig. 1). These publications set the stage for understanding the patterns of metazoan evolution, including both the

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Phylum Level Taxonomy *	Number of Decoded Spec.**	Common Name	Species Name	Size (Mb)	Year	Authors	(Some) Remarkable Genomic Features
Deuterostomia							
Chordata	291	● Round Worm	<i>C. elegans</i>	97	1998	CSC.,	The first sequenced metazoan genome. Olfactory receptor expansion.
Hemichordata	2						
Echinodermata	7	● Fly	<i>D. melanogaster</i>	180	2000	Adams et al.,	The first metazoan WGS genome. Hetero-euchromatin transition zone.
Ecdysozoa							
Nematoda	81	● Human	<i>H. sapiens</i>	3,289	2001	IHGSC., Venter et al.,	Total human genes fewer than thought.
Priapulida	1						
Nematomorpha	0						
Loricifera	0						
Kinorhyncha	0						
Onychophora	0						
Tardigrada	1						
Arthropoda	239						
Lophotrochozoa							
Mollusca	10	● Purple sea urchin	<i>S. purpuratus</i>	814	2006	SUGSC et al.,	Genes associated with vision, balance, and chemosensation in urchin.
Annelida	2						
Brachiopoda	1	● Starlet sea anemone	<i>N. vectensis</i>	357	2007	Putnam et al.,	Ancient metazoan genome complement and organization
Cycliophora	0						
Chaetognatha	0	● Placozoa	<i>T. adhaerens</i>	98	2008	Srivastava et al.,	Diversity of developmental genes more than cell types of this organism
Phoronida	0						
Bryozoa (Ectoprocta)	0	● Schistosoma	<i>S. mansoni</i>	363	2009	Berriman et al.,	Micro exon and unusual intron size distribution
Entoprocta	0						
Acanthocephala	0	● Demosponge	<i>A. queenslandica</i>	167	2010	Srivastava et al.,	Six hallmarks of animal multicellularity and the evolution of relevant genes.
Gastrotricha	0						
Gnathostomulida	0						
Nemertea	0						
Rhombzoa	0	● Owl limpet	<i>L. gigantea</i>	348			
Orthonectida	1	● Polychaeta	<i>C. teleta</i>	324	2012	Simakov et al.,	Multiple duplications of Hox complements in the leech.
Rotifera	2	● Freshwater leech	<i>H. robusta</i>	228			
Platyhelminthes	29	● Bdelloid rotifer	<i>A. vaga</i>	224	2013	Flot et al.,	Intragenomic synteny and ameiotic evolution
Bilateria							
Xenacoelomorpha	0	● Comb jelly	<i>M. leidyi</i>	150	2013	Ryan et al.,	Mesodermal genes absent from Ctenophore genome
		● Comb jelly	<i>P. bachei</i>	156	2014	Moroz et al.,	Independent evolution of the nervous system
Non-Bilateria							
Cnidaria	10	● Lingula	<i>L. anatina</i>	425	2015	Luo et al.,	Expansion of chitin synthase corresponding to the shell formation.
Placozoa	1	● Water bear	<i>H. dujardini</i>	212	2015	Boothby et al.,	
Ctenophora	2	● Acornworm (Atlantic)	<i>S. kowalevskii</i>	758	2015	Simakov et al.,	Deuterostome novelties and the pharyngeal cluster
Porifera	1	● Acornworm (Pacific)	<i>P. flava</i>	1229			
		● Orthonectid	<i>I. linei</i>	43	2016	Mikhailov et al.,	Elemental genes of the metazoan sensory systems

Fig. 1. History of published metazoan genomes categorized at the phylum level. The left two columns show the phylum level taxonomy of metazoan and the rough number of decoded genomes. The right four columns show the history of published metazoan genomes, with a citation of the first published paper for a genome for each phylum. The correspondence between the left two columns and right four columns is shown by the colored dots. The number of available genomes (at NCBI) is clearly biased toward Chordata (291), Nematoda (81), Arthropoda (239) and Platyhelminthes (29). On the other hand, the genomic data for two phylum groups symbolized here by “A” and “B” highlighted by dark gray are still very sparse. References for each paper in the figure as follows: *C.elegans* (C. elegans Sequencing Consortium, 1998), *D. melanogaster* (Adams et al., 2000), *H. sapiens* (Lander et al., 2001), *S. purpuratus* (Sodergren et al., 2006), *N. vectensis* (Putnam et al., 2007), *T. adhaerens* (Srivastava et al., 2008), *S. mansoni* (Berriman et al., 2009), *A. queenslandica* (Srivastava et al., 2010), *L. gigantea*, *C. teleta* and *H. robusta* (Simakov et al., 2013), *A. vaga* (Flot et al., 2013), *P. bachei* (Moroz et al., 2014), *M. leidyi* (Ryan et al., 2013), *L. anatina* (Luo et al., 2015), *H. dujardini* (Boothby et al., 2015), *S. kowalevskii* and *P. flava* (Simakov et al., 2015) and *I. linei* (Mikhailov et al., 2016).

origin of multicellularity and its diversification into the modern clades. In this review we discuss the insights from animal comparative genomics analysis, in particular focusing on metazoan-level evolution and the genomic processes accompanying those transitions.

2. Uncovering the ancient urmetazoan genome

Our understanding of the metazoan genetic complement relies heavily on the comparative analysis of the genomes of several key species: human (Lander et al., 2001; Venter et al., 2015), the fly *Drosophila melanogaster* (Adams et al., 2000), the nematode *Caenorhabditis elegans* (C. elegans Sequencing Consortium, 1998), the cnidarian *Nematostella vectensis* (Putnam et al., 2007), and the sponge *Amphimedon queenslandica* (Srivastava et al., 2010), as well as the outgroup (non-metazoan) species such as the most closely related group of ophisthokonts *Monosiga brevicollis* (King et al., 2008) and *Capsaspora owczarzaki* (Suga et al., 2013), followed by the fungi *Saccharomyces cerevisiae* (Engel et al., 2014) and the amoebazoan *Dictyostelium discoideum* (Eichinger et al., 2005). With contributions from expressed sequence tags (EST) studies (Kortschak et al., 2003; Kusserow et al., 2005), the nature of ancestral metazoan complexity emerged, deduced from the high degree of conservation of the gene family complements in contemporary animals. This complexity is

reflected by the presence of almost full gene family complement, such as the major toolkit genes Wnt (Kusserow et al., 2005), Hox (Schierwater and Kuhn, 1998), and T-box (Agulnik et al., 1995) families, in modern representatives of the earliest branching lineages, such as sponges, *Trichoplax*, and cnidarians. Initial studies on partial gene sets (Raible et al., 2005; Rogozin et al., 2003; Roy and Gilbert, 2005) combined with whole genome studies (Putnam et al., 2007; Raible et al., 2005; Srivastava et al., 2010) also revealed striking conservation in gene (exon-intron boundary) structure, domain architecture, and gene linkage conservation (synteny) (Table 1) in the metazoan ancestor. This hinted at a very high selective pressure to

Table 1
Inferred genomic features of the ancestral metazoan genome.

Genomic feature	Inferred ancestral values
Presumptive genome size	~300 Mb
Gene family number	7000–8000
Total gene number	> 20,000
Average exon count	3–4
Repeat content	~30%
Macro-syntenic linkage groups	~10–17
Micro-syntenic linkage groups	~ 400

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