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Echinoderm systems for gene regulatory studies in evolution and development

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One of the main challenges in Evolutionary Developmental Biology is to understand to which extent developmental changes are driven by regulatory alterations in the genomic sequence. In the recent years, the focus of comparative developmental studies has moved towards a systems biology approach providing a better understanding of the evolution of gene interactions that form the so called Gene Regulatory Networks (GRN). Echinoderms provide a powerful system to reveal regulatory mechanisms and within the past decade, due to the latest technological innovations, a great number of studies have provided valuable information for comparative GRN analyses. In this review we describe recent advances in evolution of GRNs arising from echinoderm systems, focusing on the properties of conserved regulatory kernels, circuit co-option events and GRN topological rearrangements.

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Introduction

Since the discovery of pronuclear fusion by Fol and Boveri's experiments on the developmental fate of polyspermic eggs, the sea urchin embryo has provided a powerful tool for the study of the role of genome activities during development (reviewed in [1]). After the sequencing of the purple sea urchin genome [2], the process of specification of the endomesodermal territories has been extensively studied in various sea urchin species and has led to the most exhaustive characterization of a Gene Regulatory Network (GRN) for any developmental system (reviewed in [3]). These systems level studies demonstrate the power of developmental GRNs in describing the causal progression of regulatory states (generated by a unique combination of transcription factors, TF) in embryonic space and time, necessary to specify different cell types and ultimately body plans, by providing testable predictions that are not resolvable with simplistic views of gene regulation [4]. They also highlight the potential of comparative GRN approaches to study evolution of specification processes and body plans, providing an explanation of how changes in genome sequence can cause changes in development (reviewed by [5••]).

Echinoderm embryos provide a rich source of morphological variation necessary to address relevant evolutionary developmental (evo-devo) questions such as the evolution of novelties. Of the five classes of echinoderms, four of them, namely Echinoidea, Holothuroidea, Asteroidea and Ophiuroidea, have at least one experimentally accessible species displaying feeding larvae for which embryological, molecular and, more recently, transcriptomic and genomic information is available (see Figure 1 and Table 1 for a summary). The groups of echinoderms have also excellent fossil records, which, combined with molecular phylogenies, allowed to resolve phylogenetic relationships among them and estimate divergent times [6,7]. These features place echinoderm systems in the position to greatly contribute to evo-devo, particularly from a gene regulation point of view. This potential has been already well illustrated by the comparison of the GRNs controlling endomesoderm specification in sea urchins and sea stars [8–10] and, together with the up-to-date technological advances in genomics and transcriptomics, has encouraged in very recent years the molecular exploration of additional echinoderm species. This minireview aims to highlight the most recent advances in echinoderm developmental studies with particular emphasis on those that involve GRN approaches and echinoderm species other than the 'classic' sea urchin systems (euechinoids).

Axis determination in sea urchin and redeployment of signaling cassettes

In echinoderms, while the animal vegetal axis is maternally established, the dorsal–ventral (also called aboral–oral) axis and left–right axis are determined much later in development. In the last years, significant progress has been made in the characterization of the GRNs specifying ectodermal territories in the sea urchin [11–14]. Moreover, the understanding of the left–right asymmetry, starting from the early anisotropy induced by the TGF-β ligand Nodal until the formation of the adult rudiment at the left side of the feeding larvae, is rapidly increasing