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Review article

## Echinoderm development and evolution in the post-genomic era

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### ABSTRACT

The highly recognizable animals within the phylum Echinodermata encompass an enormous disparity of adult and larval body plans. The extensive knowledge of sea urchin development has culminated in the description of the exquisitely detailed gene regulatory network (GRN) that governs the specification of various embryonic territories. This information provides a unique opportunity for comparative studies in other echinoderm taxa to understand the evolution and developmental mechanisms underlying body plan change. This review focuses on recent work that has utilized new genomic resources and systems-level experiments to address questions of evolutionary developmental biology. In particular, we synthesize the results of several recent studies from various echinoderm classes that have explored the development and evolution of the larval skeleton, which is a major feature that distinguishes the two predominant larval subtypes within the Phylum. We specifically examine the ways in which GRNs can evolve, either through *cis* regulatory and/or protein-level changes in transcription factors. We also examine recent work comparing evolution across shorter time scales that occur within and between species of sea urchin, and highlight the kinds of questions that can be addressed by these comparisons. The advent of new genomic and transcriptomic datasets in additional species from all classes of echinoderm will continue to empower the use of these taxa for evolutionary developmental studies.

### 1. Introduction

The sea urchin has been a potent model system for developmental biologists and biochemists for over a century, producing key insights into fundamental processes such as fertilization (Santella et al., 2012), cell cycle control (Yanagida, 2014; Dorée and Hunt, 2002), embryonic patterning (Molina et al., 2013; Annunziata et al., 2014; Angerer et al., 2011), including the regulative nature of early development (Angerer and Angerer, 1999), and the complex character of *cis*-regulatory control sequences (Yuh et al., 2004, 2001; Ransick and Davidson, 2006; Davidson, 1999). A key contribution of sea urchin research over the last several decades has been to describe early development using a hierarchical network of regulatory genes. Such gene regulatory networks (GRNs) explain the regulatory interactions that control successive stages of specification and differentiation (Davidson et al., 2002a, 2002b; Oliveri et al., 2008; Andrikou et al., 2015; Saunders and McClay, 2014). The GRN governing sea urchin embryogenesis is the most complete such network described to date, and portions of the network have reached a level of completeness allowing the generation of a computational boolean model in which *in silico* perturbations can predict known experimental outcomes (Peter et al., 2012).

The characteristics that make sea urchins an attractive model to developmental biologists - namely the ease of acquiring large quantities

of eggs and synchronized developing embryos, visual transparency, and ease of manipulation - are shared by many other species in the phylum Echinodermata. Given the experimental accessibility of these species and the relative strength of the sea urchin model, recent work has leveraged the intricate knowledge of sea urchin developmental regulatory interactions as a basis for evolutionary comparisons within this phylum. This review focuses, in particular, on how recent genomic data has enabled systems-level inquiries from these species which have led the way in our understanding of evolution of GRN for development.

### 2. Echinoderms: a rich disparity of body plans

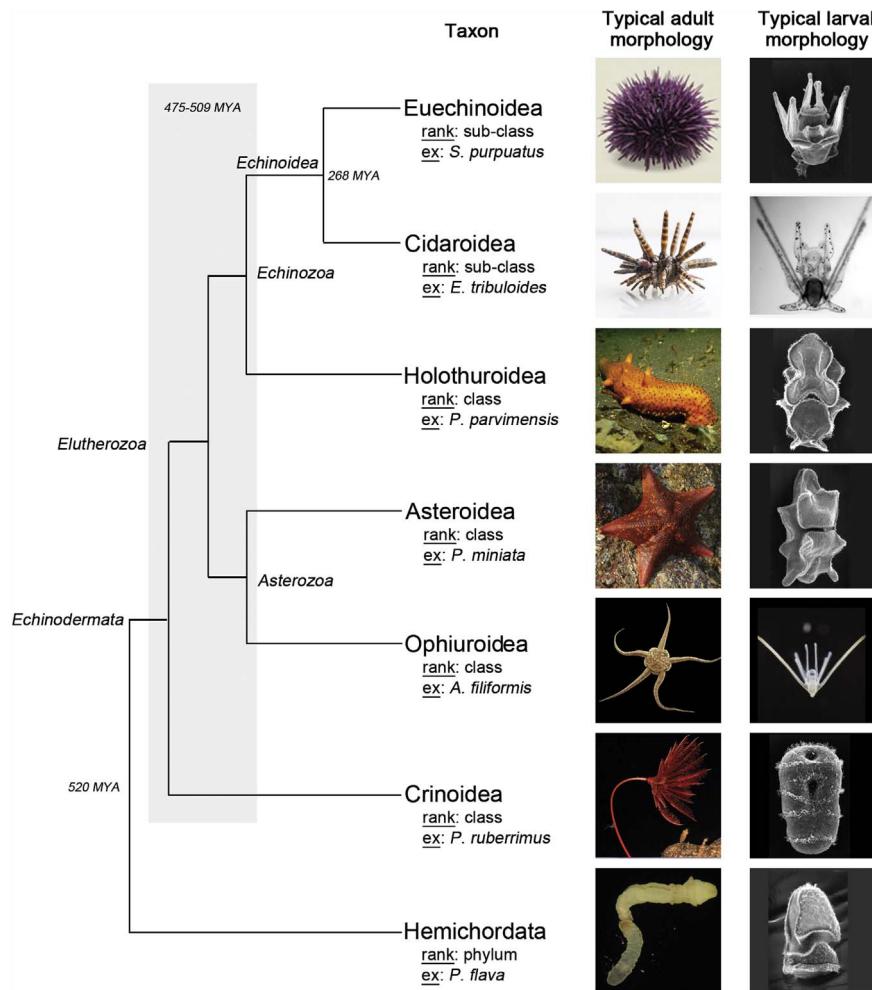
Echinoderms belong within the grouping of deuterostome animals, which only includes two other phyla; Chordata and Hemichordata. The echinoderms and hemichordates are further grouped together as the Ambulacraria (Fig. 1). There is a rich fossil record of echinoderms, which informs our current understanding of the evolution of this phylum. The earliest echinoderms are thought to have emerged in the Cambrian around 530–524 MYA (Smith, 1988). Crinoids, both stalked (sea lilies) and unstalked (feather stars), most likely diverged from the other echinoderm classes between 485 and 515 MYA (Rouse et al., 2013), however there are few living examples, and these tend to be found in deep water making them problematic for detailed functional

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**Fig. 1.** Phylogenetic relationships and example adult and larval morphologies within the Ambulacraria. Asterozoan topology, the consensus view of relationships within the echinodermata, is highlighted. Branch lengths are not drawn to scale. The images presented do not, in all cases, correspond to the example species cited. Photo credits: Adult Euechinoidea and Cidaroid are © Ann Cutting, Caltech; Holothuroidea is © Richard Ling/[www.rling.com](http://www.rling.com); Asteroidea is © Jerry Kirkhart, Los Osos, CA; Ophiuroidea is © Hans Hillewaert; Crinoidea is © NOAA Okeanos Explorer Program, INDEX-SATAL 2010; and Hemichordata is © Moorea Biocode / [calphotos.berkeley.edu](http://calphotos.berkeley.edu) 4444 4444 0513 0997. Cidarioidea larval image is adapted from [Bennett et al. \(2012\)](#), all other whole (SEM) images of echinoderm and tornaria larvae are © T.C. Lacalli and T.H.J. Gilmour ([studies. The other four classes of echinoderms form a clear grouping known as the Eleutherozoa, which recent phylogenomics suggests separated into the four classes within a 5 Myr window around 480 MYA \(\[Pisani et al., 2012\]\(#\); \[Telford et al., 2014\]\(#\)\). This rapid, ancient radiation has made it difficult to establish the relationship between the classes. Recently however, extensive genomic information has led to the congruence of the grouping sea stars and brittle stars into one clade, called the Asterozoa and sea urchins and sea cucumbers to another, termed the Echinozoa \(\[Telford et al., 2014\]\(#\); \[Reich et al., 2015\]\(#\)\). Within the echinoids, there are two broad taxa of sea urchin, the Cidarioidea \(pencil urchins, e.g. \*Eucidaris tribuloides\*\), and Euechinoidea which comprises the thin spined sea urchins represented by well known model species \(e.g. \*S. purpuratus\*, \*Lytechinus variegatus\*, \*Paracentrotus lividus\*\) as well as the lesser studied sand dollars \(e.g. \*Peronella japonica\*\). It is apparent, even to someone with just a cursory knowledge of these animals, that there is an extraordinary body plan diversity among the classes of adult echinoderms. In contrast, however there has been little intraclass deviation in body plans in the almost 500 million years since their origin.](http://University of Saskatchewan n.d.</a>).</p>
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All echinoderms also develop through a larval stage, which ancestrally was a feeding, planktotrophic larva, but has repeatedly and independently evolved in close sister taxa to non-feeding lecithotrophic forms ([Puritz et al., 2012](#); [Raff and Byrne, 2006](#)). The feeding larval forms are also highly disparate between the classes. Sea stars and sea

cucumbers form dipleurula like larval form (called a bipinnaria in sea stars and auricularia in sea cucumbers) ([Nakano et al., 2003](#); [Byrne et al., 2007](#)), and while the larva of the sea lily is non-feeding, it nonetheless also forms a dipleurula larva ([Nakano et al., 2003](#); [Fig. 1](#)). This larva-type is characterized by having two loops of ciliary bands that transverse the ectoderm. The similarity of this larval type to the tornaria larvae of hemichordates suggests that this larval form is basal among the Echinoderms, and possibly also Ambulacraria and hence more broadly the entire deuterostome clade ([Cannon et al., 2014](#); [Cameron et al., 2000](#)). Sea urchins and brittle stars, by contrast, have a pluteus larva (echinopluteus in sea urchins and ophiopluteus in brittle stars) that have a single ciliary band around the oral ectoderm and a large, dominant larval skeleton. It is the larval skeleton that gives the plutei their striking armed phenotype. As sea urchins and brittle stars are not sister taxa, the origin of these larval types is difficult to resolve, but for now the most parsimonious explanation is that the plutei evolved independently from dipleurula larval forms within the lineages leading to the Echinozoa and Ophiuroidea ([Morino et al., 2016](#)).

This disparity comprises a rich natural source of large scale body plan changes that permit investigation of deep-time divergence of dramatic body plan evolution. This, coupled with the extraordinary analyses of GRNs in sea urchins, provides an unparalleled potential to understand how GRNs have evolved for such developmental change. Additionally, smaller scale comparisons made within populations or

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