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Gene expression during echinoderm metamorphosis

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Metamorphosis is a remarkable process in echinoderms, transforming a bilaterally symmetrical planktonic larva into a radially symmetrical benthic adult. This shift in habitat involves functional and anatomical changes in virtually every organ system (Bury, 1895; MacBride, 1914; Okazaki, 1975). Although metamorphosis is a crucial process in echinoderm development, we know relatively little about it. Furthermore, most of what we do know concerns sea urchins, and even less information is available about metamorphosis in other echinoderms. We have examined the expression of regulatory and structural genes during metamorphosis in several different echinoderm species (Lowe & Wray, 1997 and unpublished results). These data, together with those from several recent studies concerning additional genes (reviewed in Wray & Lowe, 2000), are beginning to shed new light on this complex and important process in echinoderm development.

The overt transformation from swimming larva to settled juvenile is quite rapid in echinoderms (Cameron & Hinegardner, 1978), requiring less than half an hour in many species. The complete process of metamorphosis takes much longer, however (Okazaki, 1975; Gosselin & Jangoux, 1998). Extensive preparations begin several days to weeks before settlement (MacBride, 1914; Okazaki, 1975), depending upon the species and upon environmental conditions (Strathmann *et al.*, 1992). During this preparatory phase, initially small populations of ectodermal and mesodermal cells fated to become the adult proliferate, differentiate and undergo complex morphogenetic movements to form the imaginal rudiment (MacBride, 1914; Okazaki, 1975). The rudiment is more complex than the larva in several important ways: it contains a greater number of cell types, it is the first place where true tissues form, and it contains the first well-organised nervous system (Okazaki, 1975; Chia & Burke, 1978).

Echinoderm development requires pattern formation systems for two completely different bodies: a bilateral larva and a radial adult. The relatively simple bilateral larval body is patterned during embryogenesis, primarily through a series of cell–cell interactions that have been studied extensively (reviewed in Davidson *et al.*, 1998). Patterning of the radial adult body occurs much later, within the imaginal rudiment (see Bury, 1895; MacBride, 1914; Lowe & Wray, 1997). The transition between the two symmetry systems involves a brief period of left–right asymmetry, during which the imaginal rudiment is established on the left side of the larval body.

These shifts in anatomical symmetry are reflected in changing patterns of gene expression in sea urchins, the group from which the vast majority of data have been collected (reviewed in Wray & Lowe, 2000). Maternal and early zygotic gene expression is radially distributed about the animal–vegetal axis, since the dorsoventral axis is not established until several hours after fertilisation (reviewed in Davidson *et al.*, 1998). Beginning with gastrulation and into the early larva many genes are expressed in bilaterally symmetrical domains (reviewed in Coffman & Davidson, 1992; Kingsley *et al.*, 1993). The first morphological signs of left–right asymmetry appear after gastrulation (Okazaki, 1975). The earliest known left–right asymmetrical gene expression involves *Distal-less* (Lowe & Wray, 1997), which encodes a homeodomain transcription factor. This gene is initially expressed in just a few cells within the oral ectoderm; later, this small patch of ectoderm invaginates to form the vestibule, the ectodermal component of the imaginal adult rudiment. Because *Distal-less* expression begins prior to any anatomical sign of morphogenesis or differentiation of the vestibule, it may be playing a role in the specification of vestibular cell fate.

After the vestibule begins to invaginate, two additional regulatory genes are expressed – *Not* and *Brachyury* (Peterson *et al.*, 1999) – both of which enocode transcription factors. Both these genes are first expressed within the vegetal plate of embryos, but are upregulated much later specifically within the invaginating ectodermal cells of the vestibule. *Brachyury* is also expressed in the left and right hydrocoeles (mesocoeles) in a bilaterally symmetrical pattern during formation of the imaginal rudiment. Both *Distal-less* and *Brachyury* are expressed in an asymmetrical pattern, exclusively within the left hydrocoele at this time. Expression of neither gene begins before visible signs of left–right asymmetry, however, so they probably lie downstream of the patterning event that establishes the initial asymmetry.

At the completion of vestibular invagination, the

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ectodermal sheet comes into contact with the underlying left hydrocoele and both cell layers undergo extensive proliferation (Okazaki, 1975; Chia & Burke, 1978). It is within these juxtaposed cell layers that the five-fold radial symmetry of the adult is established. The first anatomical sign of radial symmetry is the appearance of buds which will develop into the five primary podia (Bury, 1895; MacBride, 1914). As expected, several genes are expressed in radially symmetrical domains within the developing rudiment (reviewed in Wray & Lowe, 2000). For example, in late-stage rudiments just prior to metamorphosis, both *Distal-less* and *Orthodenticle*, another transcription factor, are expressed within the five primary podia quite strongly (Lowe & Wray, 1997). Expression of *engrailed*, yet another transcription factor, is also organised in a radially symmetrical pattern in the late-stage rudiment, throughout the coelomic compartments and the entire central nervous system (E. Popodi & R. Raff, personal communication). The structural gene *msp130*, which encodes a component of the spicule matrix in sea urchins, is expressed in a radially symmetrical pattern at sites of skeletogenesis (Parks *et al.*, 1988).

Hox gene expression is quite active during rudiment formation in sea urchins. *Hox-3* is expressed interadially within the circle of primary podia, probably within the tooth sacs (Arenas-Mena *et al.*, 1998). Although localisations for the other sea urchin *Hox* genes have not been published, RNase protection assays demonstrate that the entire *Hox* complex is upregulated during development of the imaginal adult rudiment (Arenas-Mena *et al.*, 1998). Indeed, only two genes of the *Hox* complex are expressed in embryos or larvae at all. This result suggests that the primary function of the *Hox* complex in urchins is not patterning the embryo, as is the case in arthropods and chordates, but instead patterning the post-embryonic adult body plan.

Following overt metamorphosis, the juvenile sea urchin looks superficially like a miniature adult. There are several additional processes, however, that must be completed before metamorphosis is complete (Gosselin & Jangoux, 1998). Most immediately important among these are formation of the definitive adult mouth and anus and differentiation of the juvenile gut. Much of the formation of the adult skeleton occurs after metamorphosis (Gordon, 1926), as is the case for several internal organs (Chia & Burke, 1978). These processes undoubtedly require activating regulatory and structural genes in precise patterns. Little is known about gene expression following metamorphosis. Some of the regulatory genes active during rudiment formation are also expressed just after metamorphosis, but often in more spatially restricted patterns (reviewed in Wray & Lowe, 2000). For example, *Distal-less* is expressed at the termini of podia and spines, and *Orthodenticle* is expressed within the jaw apparatus, the peristomial ectoderm and podia (Lowe & Wray, 1997).

As methods and probes for examining gene expression in echinoderms become more accessible and widely applied, it should become possible to construct a much more detailed understanding of gene expression during metamorphosis. Over the next few years we expect to learn much more about which genes are expressed during this crucial phase of echinoderm development, what roles they play in the development of adult tissues and structures, and how the expression of these genes differs among echinoderm species.

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