<Further Development 23_10>

Metamorphosis of the Pluteus Larva

Sea urchins undergo complete metamorphosis, forming a “primary larva”—the pluteus—which is later jettisoned pretty much in its entirety. Almost the entire body of the adult sea urchin comes from the left coelomic sac of the pluteus archenteron. The larval skeleton is abandoned, while the rest of the larval body undergoes programmed cell death, providing raw materials for juvenile growth. As the pluteus forms, the top of the archenteron meets the blastocoel wall. Here, the secondary mesenchyme cells form the right and left coelomic pouches (see Figure 11.5, 13.5 hours). Under the influence of Nodal protein, the right coelomic sac remains rudimentary while the left coelomic sac undergoes extensive development to form the structures of the adult sea urchin. This growth involves activating BMP signaling on the left side. The small micromeres, which give rise to the germ cells, are attracted to the coelomic sacs by chemoattractant factors synthesized by means of a gene regulatory network similar to that of the *Drosophila* eye (Yajima and Wessels 2012**;** Campanale et al. 2014; Martik and McClay 2015). These primordial germ cells are preferentially retained by the left coelomic pouch (Luo and Su 2012; Warner et al. 2012).

The left sac eventually splits into three smaller sacs. An invagination from the ectoderm fuses with the middle sac to form the imaginal rudiment**,** and only the aboral epidermis is derived from the larval dermis. This rudiment develops a fivefold (pentaradial) symmetry (Figure 1), and skeletogenic mesenchyme cells enter the rudiment to synthesize the first skeletal plates of the shell. The left side of the pluteus in effect becomes the future oral surface of the adult sea urchin (Bury 1895; Aihara and Amemiya 2001; Minsuk et al. 2009). During metamorphosis, the larva settles on the sea floor and the imaginal rudiment separates from the larva, which then degenerates. As we will see in Chapter 24, the cues for larval settlement often include a mixture of environmental factors such as photoperiod, turbulence, and chemicals released by potential food sources. In some sea urchin species, the shear force generated by turbulence enables the larvae to sense and respond to chemicals emanating from algae and bacteria (indicating that food for the adults is abundant) (Rowley 1989; Gaylord et al. 2013; Nielsen et al. 2015). While the imaginal rudiment (now called a juvenile) is re-forming its digestive tract, it is dependent on the nutrition it receives from the disintegrating larval structures.

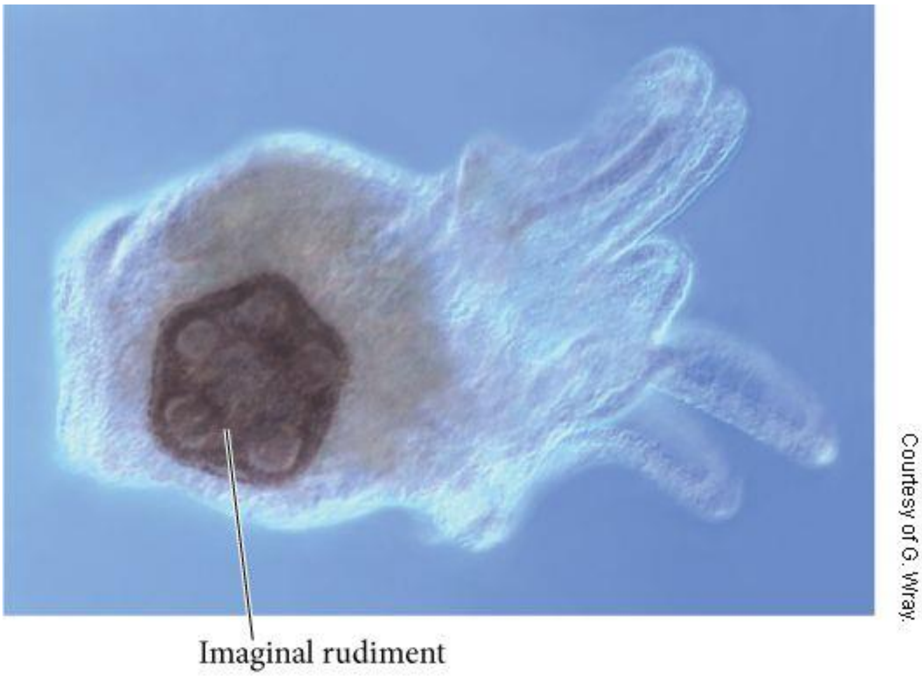

Figure1 The imaginal rudiment growing in the left side of the pluteus larva of a sea urchin. The rudiment will become the adult sea urchin, while most of the larval stage will be dissolved. The fivefold symmetry of the rudiment is obvious.

The pentaradial symmetry of adult echinoderms is unique and distinguishes them from the many bilaterally symmetrical animals. Note, however, that pluteus larvae *are* bilaterally symmetrical—evidence that echinoderms share a common ancestor with the bilaterally symmetrical chordates (Zamora et al. 2012, 2015). The sea urchin larvae and adult differ dramatically. Indeed, the pluteus larva is a free-swimming planktonic dispersal stage with no sexual reproductive capacity, whereas the adult grazes on algae on the sea floor and produces thousands of gametes. It is also interesting that, like amphibians, echinoderms such as sea urchins use thyroid hormones to cue metamorphosis (Chino et al. 1994; Heyland and Hodin 2004).

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