<Further Development 11_05>

Evolution by Subroutine Co-option

The skeletogenic portion of the micromere gene regulatory network shown in Figure 11.13B appears to have arisen from the recruitment of a network subroutine that in most echinoderms (including sea urchins) is used in making the adult skeleton (Gao and Davidson 2008; Erkenbrack and Davidson 2015). The co-option of subroutines by a new lineage is one of the ways evolution occurs. It happens that the GRN of sea urchin micromeres is very different from that in other echinoderm embryos. Only in sea urchins has the skeletogenic subroutine come under the control of the genes that specify cells to the micromere lineage; in all other echinoderms, skeletogenesis is activated late in development. The most important evolutionary events were those placing the skeletogenic genes *Alx1* and *Ets1* (necessary for adult skeletal development) and *Tbr* (used in later larval skeleton formation) under the regulation of the *Pmar1-HesC* double-negative gate. This occurred through mutations in the *cis*-regulatory regions of these genes. Thus, the skeletogenic properties that distinguish the sea urchin micromeres appear to have arisen through the recruitment of a preexisting skeletogenic regulatory system by the micromere lineage gene regulatory system.