

## CHAPTER 14

- 1) Most significantly the appearance of cell adhesion and cell communication molecules which would allow for the coordination of the cellular diversification that accompanies multicellularity. As secondary events the emergence of Hox genes and of cell signaling associated transcription factors.
- 2) The phylotypic state is characterized by a stereotypical segmented axial organization. This basic segmental organization is the basis for the diversification, ruled by the Hox genes, that is the basis for the variety of animal forms. It is, probably, this very fundamental organization and its potential that constrains this stage.
- 3) The emergence of the Bicoid protein (the early anteroposterior morphogen in *Drosophila*) from a duplication of the gene *zerknüllt*, is an example of the first kind; Bicoid is only present in Diptera. (See chapter 2 for details of the function of these proteins). As for changes in gene expression that occur after gene duplication, probably the Hox genes are the best example. They also provide examples, but less dramatic examples, of protein evolution after gene duplication.
- 4) (1) Fossil record suggests that skeletal elements of a limb evolved from skeletal elements of a fin see details in Fig. 14.20. (2) Zebrafish fins end in distal rays, structures not present in tetrapod limbs, so need to discuss whether any elements of the zebrafish skeleton are equivalent to the digits in vertebrate limbs; base your arguments on evidence from comparisons of Hox gene expression patterns in fins and limbs and analysis of the enhancers that drive the expression of these genes. Investigations on embryos of a Devonian fish could include observations on the time course of skeletal development in the fin buds, analysis of Hox gene expression patterns and enhancer function.
- 5) Distalless expression is associated with the emergence of leg discs and thereby of legs. With this in mind, the answer to the question lies in the differential control of the expression of Hox genes in Diptera and Lepidoptera and the observation that if the Bithorax complex is eliminated in the *Drosophila* (Diptera) embryo, Distalless becomes expressed in every abdominal segment and leads to the appearance of leg discs. In the larvae of Lepidoptera, the expression of Ubx and abdA, the main genes of the bithorax complex expressed in the abdomen, is suppressed ventrally, allowing the expression of Distalless and the emergence of legs.
- 6) Both changes in Hox gene expression and in interpretation of the Hox code have been identified in snakes. Include *Hoxc6* and *Hoxc8* expression patterns in somites in pythons and changes in an enhancer of a *Hoxa10* target gene involved in vertebral identity in corn snakes.
- 7) Need to discuss the candidate genes *Alx4* and *calmodulin*. How were these genes identified? How could study of these candidates be taken further to pinpoint the precise genetic change that affects beak shape? – the studies on pelvic reduction in stickleback outlined in Box 14D could provide some ideas. How could changes in these candidate genes be related to the strength, timing and location of BMP signalling which has been shown to modulate beak shape in chick embryos? You should do this.
- 8) Heterochrony is, essentially a change in the timing of developmental events. This can have significant impact in the final product of a process. You have several choices of examples. One clear one is the difference in the size and organization of the digits of the foot in salamanders that live in trees, shorter and webbed, which can be explained as a result of this limb differentiating before completing the development of other species. There are others that you can find in the text and the literature. Neoteny, in which an adult manifests the shape of a larval or developmentally immature form, is another example.
- 9) The most important element here is the distinction between the generation of segments simultaneously (*Drosophila*) or over time (short germ band insects). You should discuss how there are different kinds of short germ band insects which establish a different number of segments initially and how there is a range from all (*Drosophila*) to very few (grasshoppers). Mention how the pattern progresses from anterior to posterior in all cases.

- 10) Examples are the manipulation of *Ubx* expression in the amphipod *Parhyale hawaiiensis* and the tests of the function of the snake ZRS in mouse embryos. For limitations of this technique also see discussion in Box3D in Chapter 3.