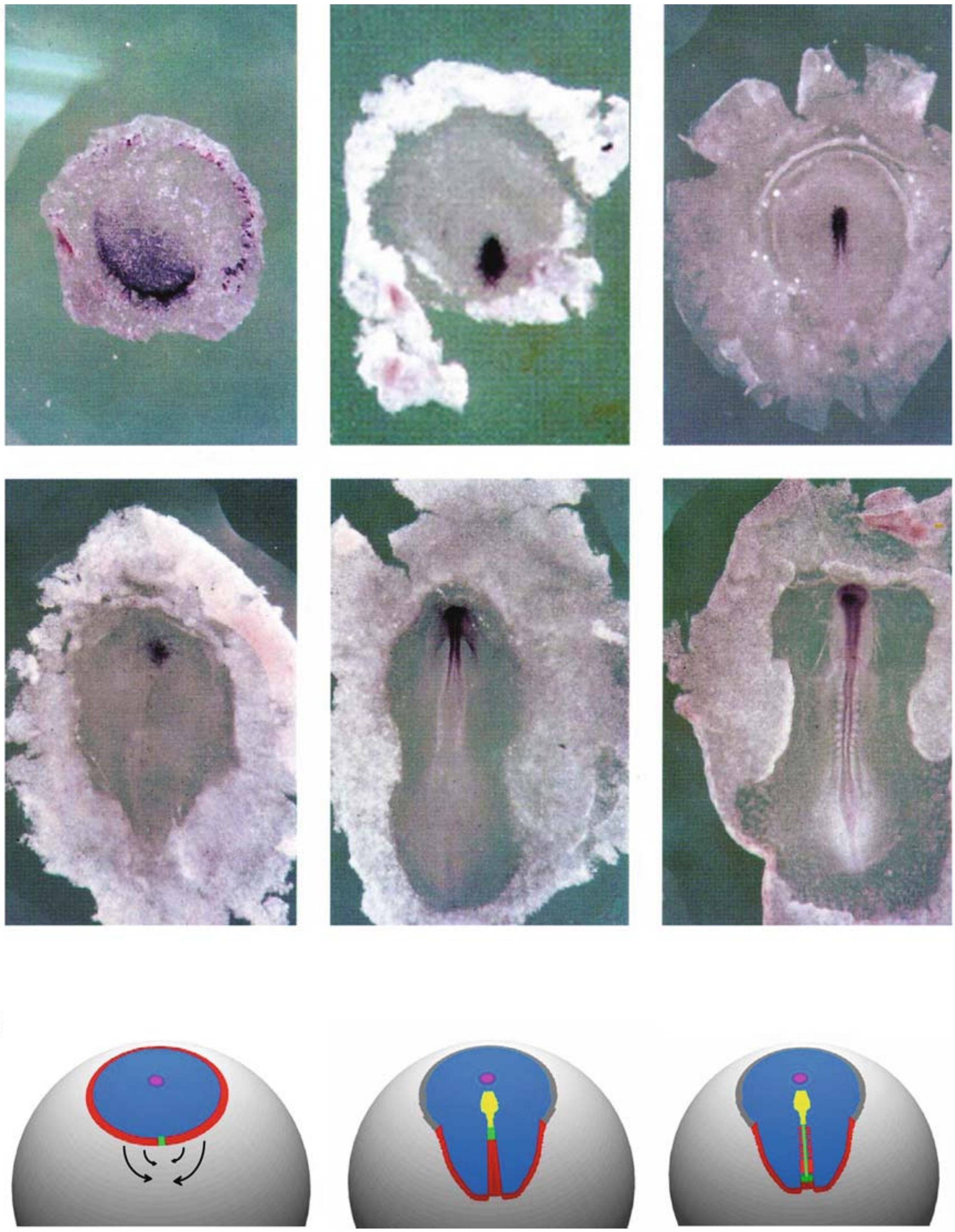
a
b,c
d
e,f
g
h,i

Chapter 12

Pattern formation in the development of higher organisms

The development of higher organisms out of a single cell is a most fascinating process. As an example, Figure 12.1 shows stages in the early development of a chick embryo. It was pointed out repeatedly that the mechanisms discussed for shell patterning are more general and of vital importance for pattern formation during embryonic development in higher organisms. In this chapter, some important steps in this development will be outlined and compared with corresponding models. In the subsequent chapter, some special biological phenomena will be discussed for which the lessons learned from the shell patterns were decisive for deriving the corresponding models.

The development of an organism is, of course, a highly complex process. It may appear hopeless to try and formulate an integral mathematically founded theory. Experiments revealed, however, that the individual steps are to some degree independent of each other. For the fruit fly *Drosophila* it has been shown that the pattern along the anteroposterior (head-to-tail) axis can be substantially modified without any effect on the dorsoventral (back-to-belly) patterning and vice versa. Different sets of genes are involved in establishing the two axes (Nüsslein-Volhard, 1996). Analogously, during the development of an arm, the anteroposterior (thumb to little finger) axis can be modified without much effect on the proximodistal axis (upper arm to digits, see Figure 12.10). Another example showing that closely

Figure 12.1. Stages in the development of a chick embryo. (a-f) The early chick embryo is a nearly flat disk located on the huge mass of yolk. Dark regions indicate a high activity of the gene *goosecoid*, a marker for the organizing region. First a crescent-like expression is seen (a) that sharpens to a small patch (b). Cells to the left and to the right of the organizing region move behind the organizer. Thus, part of the margin of the disk becomes deformed to a hair-pin-like structure, the primitive streak. The organizer, called Hensen's node, is initially still at the tip of the streak. The proper embryo emerges in a sequential process behind the organizer which moves towards the margin of the disk. Thus, new elements are added posteriorly until the tail is formed. This process goes on the expense of the primitive streak. (g-i) Schematic drawing showing the formation of the primitive streak by a hair-pin-like deformation of parts of the margin of the disk (g,h). The head lobe (yellow) is formed by an anterior movement of cells from the organizer (green). With the movement of the organizer, the primitive streak regresses in favor of the final organism (i) (for modeling, see Meinhardt, 2006 and material on the CD; photographs kindly supplied by Lydia Lemaire, see Lemaire et al., 1997)

H. Meinhardt, *The Algorithmic Beauty of Sea Shells*, 4th ed. The Virtual Laboratory,
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