Morphogenesis

Morphogenesis means the creation of structure and form, and reflects the many different types of cell behavior that help to shape tissues and organs. Cells may change their size and shape, they may adhere or disperse, they may remain quiescent or divide, they may move relative to other cells, they may fuse together and they may even die in the process of sculpting a particular developing organ. In later development, morphogenesis can be regarded as a *response* to the developmental program, i.e. a differentiated cell aware of its position in the embryo will behave in such a manner as to generate a regionally-appropriate structure. Earlier in development, however, morphogenesis is instrumental in *driving* the developmental program, e.g. by bringing cells together to undergo inductive interactions. This is illustrated by the complex morphogenetic movements of gastrulation (Section F). The cellular basis of morphogenesis is discussed in more detail in Topic A7.

Morphogenesis

The entire group of processes that mold the external and internal configuration of an embryo is included under the general term *morphogenesis*. A wide variety of phenomena can be included under the overall umbrella of morphogenetic events in the embryo. These range from establishment of the fundamental axes (e.g., anteroposterior, dorsoventral, and proximodistal), to the branching of the ducts within glands, to the formation of limbs or the intricate structure of a feather, to the complex loops and whorls on the fingertips. In many systems, *pattern formation* (laying down of the morphogenetic blueprint) is distinguished from morphogenesis (realization of the plans).

Until recently, virtually nothing was known about mechanistic basis of morphogenesis. This has changed dramatically with the discovery of the molecular basis of pattern formation in *Drosophila* and the widespread distribution of classes of genes that underlie segmentation in the vertebrate embryo.

Establishment of the fundamental body plan in *Drosophila* is under tight genetic control (see reviews by Lawrence, 1992; St. Johnston and Nüsslein-Volhard, 1992). This begins with the actions of *maternal effect genes,* which establish the anteroposterior and dorsoventral axes of the early embryo (Fig. 1-21). Products of the maternal effect genes activate zygotic *gap genes,* the products of which subdivide the embryo into several broad anteroposterior bands. The next tier in the hierarchy of morphogenetic gene expression includes the *pair rule genes*. Products of these genes define seven vertical bands, which are separated by bands that do not express these gene products. The 14 segments of the *Drosophila* embryo are defined by *segment polarity genes,* but these genes do not impart any specific characteristics to the segments. This latter function is left to the *homeotic genes,* which determine the regional characteristics of each segment, e.g., some segments will produce legs, others wings, etc. One of the major embryological themes of the early 1990s is the recognition that many of the important segmentation genes in *Drosophila* are expressed in vertebrate embryos. Numerous examples of such gene expression will be presented throughout the text.

The underlying basis for other important morphogenetic phenomena, for example the branching patterns of duct systems in glands, remains poorly understood. Whether or not the genetic basis is understood, realization of the pattern underlying morphogenesis is accomplished by employing familiar processes in special ways. These may include cell proliferation, migration, aggregation, secretion of extracellular substances, change in cell shape, and even localized cell death (Fig. 1-22).