EMERGENCE OF PATTERNS
Pattern Formation
Fate Maps

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10.5 EMERGENCE OF PATTERNS

In the beginning of this unit we had written that one of the most fascinating questions in animal development is the generation of a complex organism from a single fertilised cell the zygole. As embryonic development proceeds it involves the emergence of a pattern which shows the overall position of cells in the embryo so that the body's shape and form begins to emerge. This is followed by cell differentiation and growth.

Development is a gradual process by which a complex multicellular organism arises from a single cell (the zygote). It involves 5 major overlapping processes:

1) growth = increase in size

2) cell division= increase in number

3) differentiation = diversification of cell types

4) pattern formation = organization

5) morphogenesis = generation of shapes and structures

10.5.1 Pattern Formation

As the zygote divides it undergoes a process by which the initially equivalent (similar) cells acquire different identities which depend on their relative positions in the embryo at different times during development. As a result a well ordered structure of the developing embryo emerges. This process is known as pattern formation. **In other words pattern formation in developmental biology, is the mechanism by which initially equivalent cells located at a particular position in a developing tissue of the embryo assume complex forms and functions. Thus, what a cell will become later in the embryo depends on its position within the developing embryo**. The final fate of development of a single cell takes place in several progressive steps. For example, during development the pattern formation of the face enables the cells to know where the nose, ears, eyes have to be formed and what muscles are to be placed in the space to support the structure of the face. In animal development, pattern formation is established early in embryogenesis. This patterning during animal development in different organisms is achieved at different times by cellular and molecular mechanisms.

- The first step in pattern formation is the laying down of the body axes: i) that run from head (anterior) to tail (posterior) and ii) from back (dorsal) to the underside (ventral). Most of the animals that we are taking as examples to discuss development in this course are externally observable as bilaterally symmetrical. This means, that the left and right side of their body are mirror images of each other. The body of such types of animals have an anterio-posterier axis and a dorso- ventral axis. Both these axes are always at right angles to each other and make a coordinate on which the form of the animal is specified (see Fig.10.9).

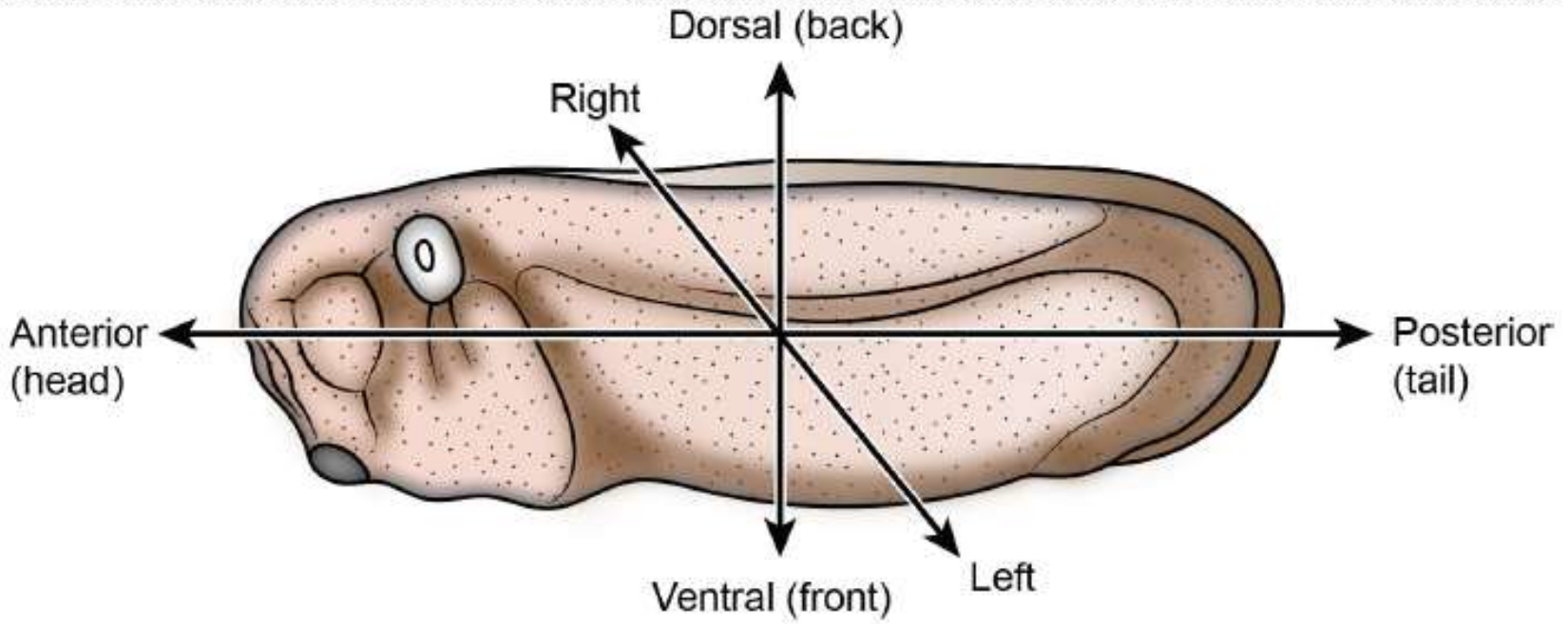

Fig.10.9: The main axes in a developing embryo of *Xenopus laevis.*

Vertebrate animal bodies have externally visible symmetry but the internal organs are not symmetrical for instance the heart is on the left side and liver on the right. These axes in the embryo are established very early in development. Several genes are involved in the establishment of axes in the embryo. Before the externally visible body axes get specified in the embryo the egg also always has a distinct polarity or orientation. At the same time that the axes are being formed in the embryo, the cells in the embryo of triploblastic animals get organized into the three different germ layers namely ectoderm (external layer), mesoderm (middle layer) and endoderm (internal layer).In the case of diploblastic, animals the cells in the embryo get organized into the two different germ layers namely ectoderm (external) and endoderm (internal). The positions of cells in the germinal layers of both diploblastic and triploblastic, embryos of the animals which are laid down during gastrula stage show their prospective fate by the end of development. During further emergence of pattern, the cells of these layers acquire different identities (become different) so that they form the different tissues and organs of the body like skin, muscle, blood cells, neural cells etc. Figure 10.10 gives a diagram of the fate of the three germ layers in animals.

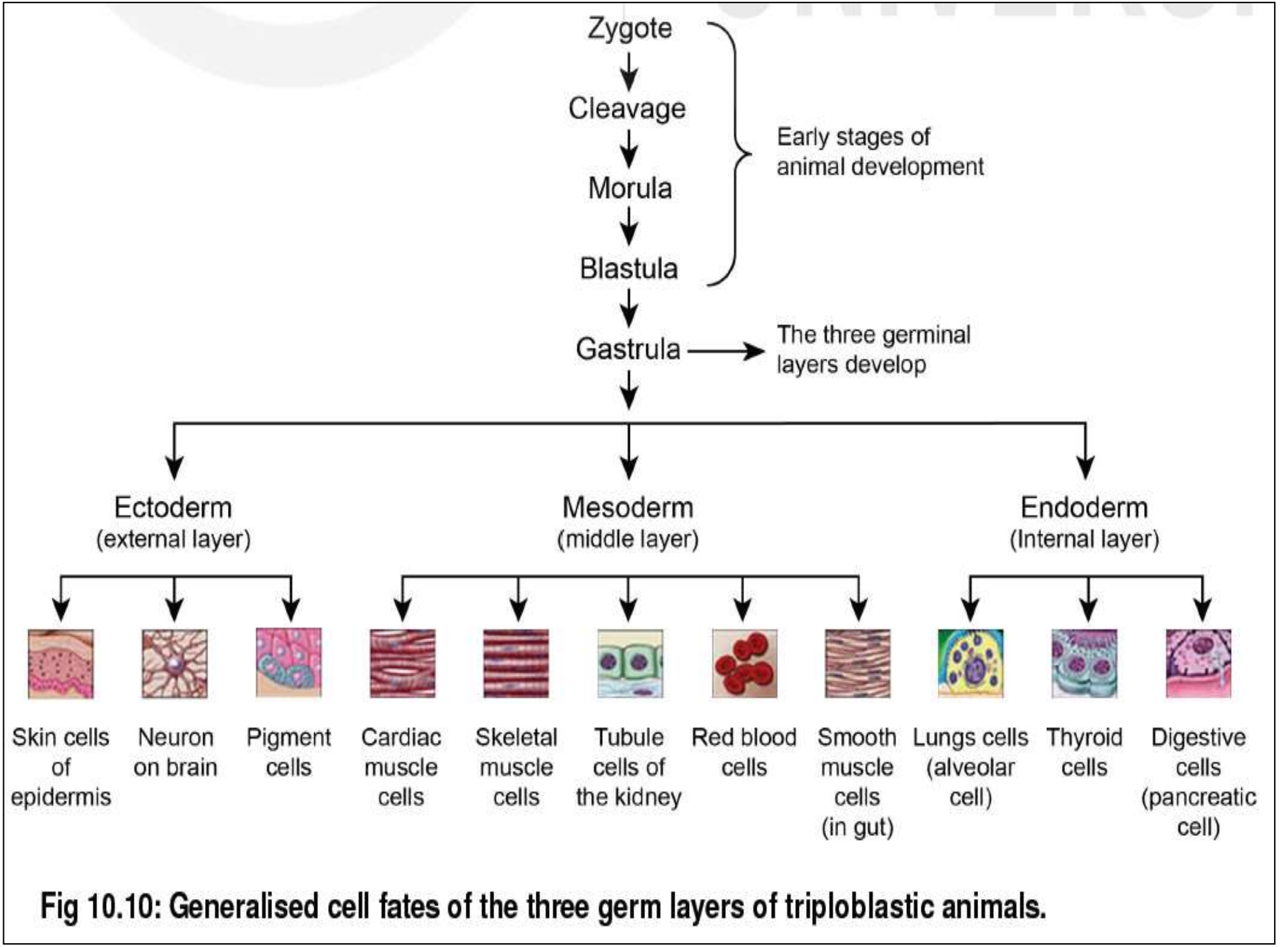

Fig 10.10: Generalised cell fates of the three germ layers of triploblastic animals.

Pattern formation can take place by two mechanisms: (i) **cell to cell interactions** also known as **inductive mechanisms** in which one type of cells induces or instructs other cells to change their behaviour and develop in a different way or to become different types of cell; (ii) **morphogenetic mechanisms** that act on previously established patterns in order to form the three dimensional tissues and organs. This process involves changes in the location of the cells, without changes in their behaviour. For instance, during gastrulation in frogs, the endoderm and mesoderm move inside the embryo from the surface. This results in the formation of the gut which is a tube within a tube structure. The embryo thus, during development undergoes remarkable changes in appearance or morphology. These changes occur due to extensive cell migration which will also cause changes in the shape of the embryo. In this process some cells undergo programmed cell death as well. We will be

10.5.2 Fate Maps

Since the early 1900s, as you will recall, experimental embryologists became interested to find out the fate of each cell in the developing embryo and what it would gave rise to in the adult animal. Initially it was not easy to trace the cell lineage (which structures will be formed from the cell and its descendants at a later stage of normal development) or cell fate of individual embryonic cells. Thus, embryologists used different techniques to label groups of cells in the early stages of embryonic development and followed their progressive development until the stage of a fully formed embryo. By using various labelling techniques of groups of cells from early stages to end of the embryo formation, embryologists were able to construct **fate maps** or diagrams of areas of the embryo for depicting the fate of the various cells during normal development. Most embryonic cells have predictable fates. Cells in different embryos of same species will develop same structures or will have the same fate. In fact, most early vertebrate embryos show remarkable similarities in their fate maps as can be seen in Figure 10.11 Fate maps can be constructed using different methods which are becoming more sophisticated with increasing technological advances. Each has its advantages and disadvantages.

TECHNIQUES USED FOR PREPARATION OF FATE MAPS

1) **Observing living embryos**: some species have embryos that have relatively small number of cells that are transparent and the development of blastomeres can be observed directly under the microscope or the cells may be naturally coloured (pigmented) so that the development can be traced following the coloured cells. E. G. Conklin in early 1900s was able to follow the development of early cells in a tunicate *Styela partita*. From his studies it was found that only one pair of blastomeres at the 8 cell stage (the posterior vegetal bastomeres) were capable of forming tail muscles. These had yellow pigment hence it was easy to follow their development. Removal of one such blastomere (B4-1) resulted in an embryo with no tail confirming Conklin's fate map of the tunicaste *Styla partita*.

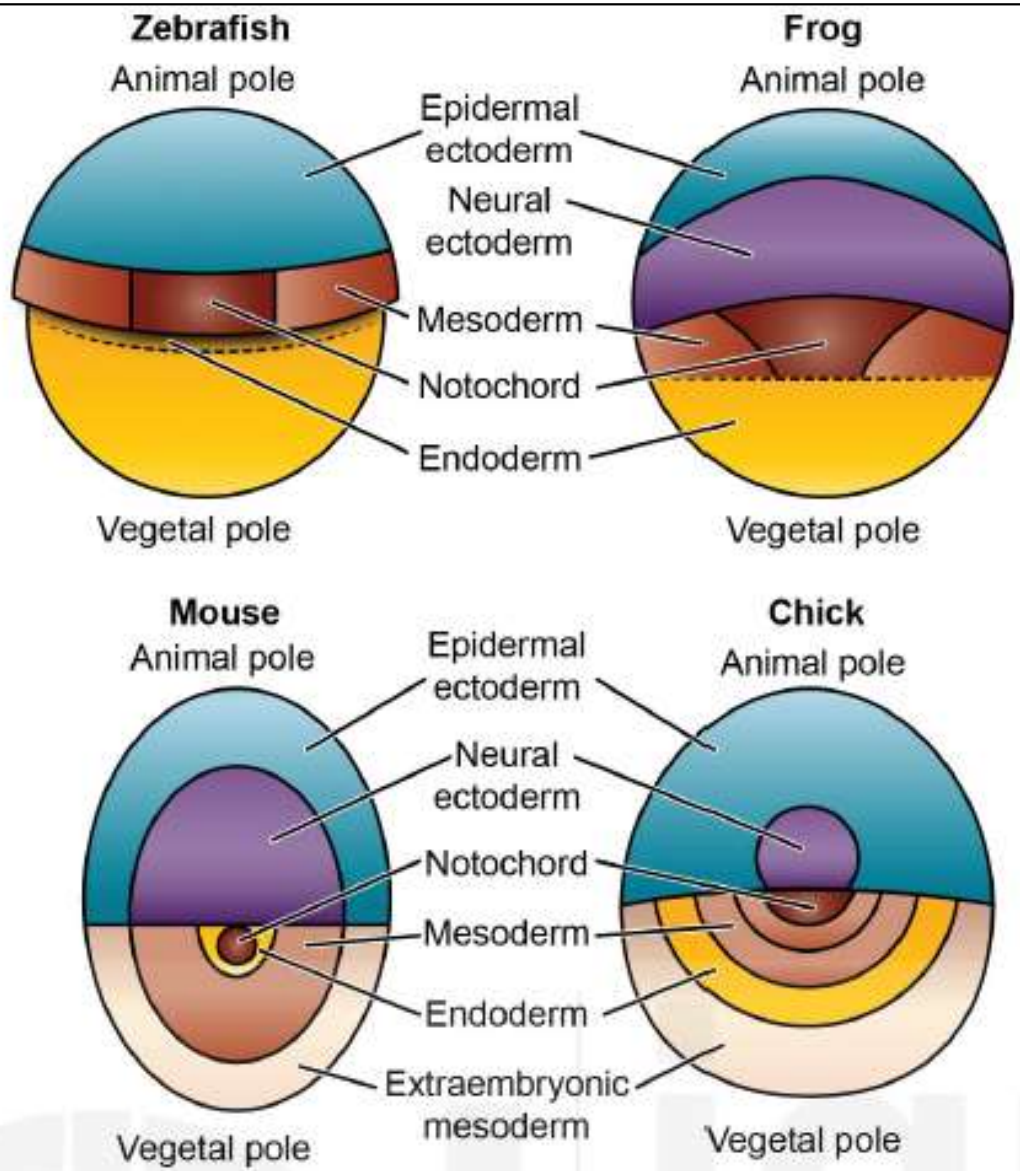

Fig.10.11: Fate maps of some vertebrate embryos in dorsal view (that is looking down on the embryo to see its back view). You can observe that there are general similarities in all. The cells that will form notochord are in the central position. Ectoderm precursors are anterior, mesoderm lateral and endoderm precursors lie posterior to the cells that make the notochord. The dashed lines show the path where the cells will move inside the embryo.

2) **Use of Dye marking**: vital dyes (dyes that do not damage the embryo but just stain the cells) are often used to trace cell lineages. Walter Vogt in 1929 used such a dye to follow the development of stained cells in newt embryos. However vital dyes get diluted over the period of cell division and become difficult to trace.

3) **Fluorescent dyes and radioactive marking**: are used to overcome the problem seen with vital dyes. Fluorescent dyes can be used that are so intense that they can be traced for a large number of cell divisions. Similarly radioactive labelling of dividing cells can also help to trace the path of the dividing embryonic cells.

3) **Genetic labelling**: This is a method of permanently labelling cells in order to follow their path in development. The best method is the formation of chimeras that are embryos created by fusion of cells from two different, but closely related species. The best example seen is of a chick quail chimera made by grafting quail embryonic cells in a chick embryo while it is still in the egg (Fig.10.12). When the chick hatches it also has quail cells in the tissue which develops from the grafted quail embryonic cells. Another method is by using genetic markers. In this case a marker gene is inserted in the nucleus. Each time the cell divides the tagged gene will also duplicate and in this way these cells that express the genetically modified gene can be traced to the cells of the embryo where the gene was inserted.

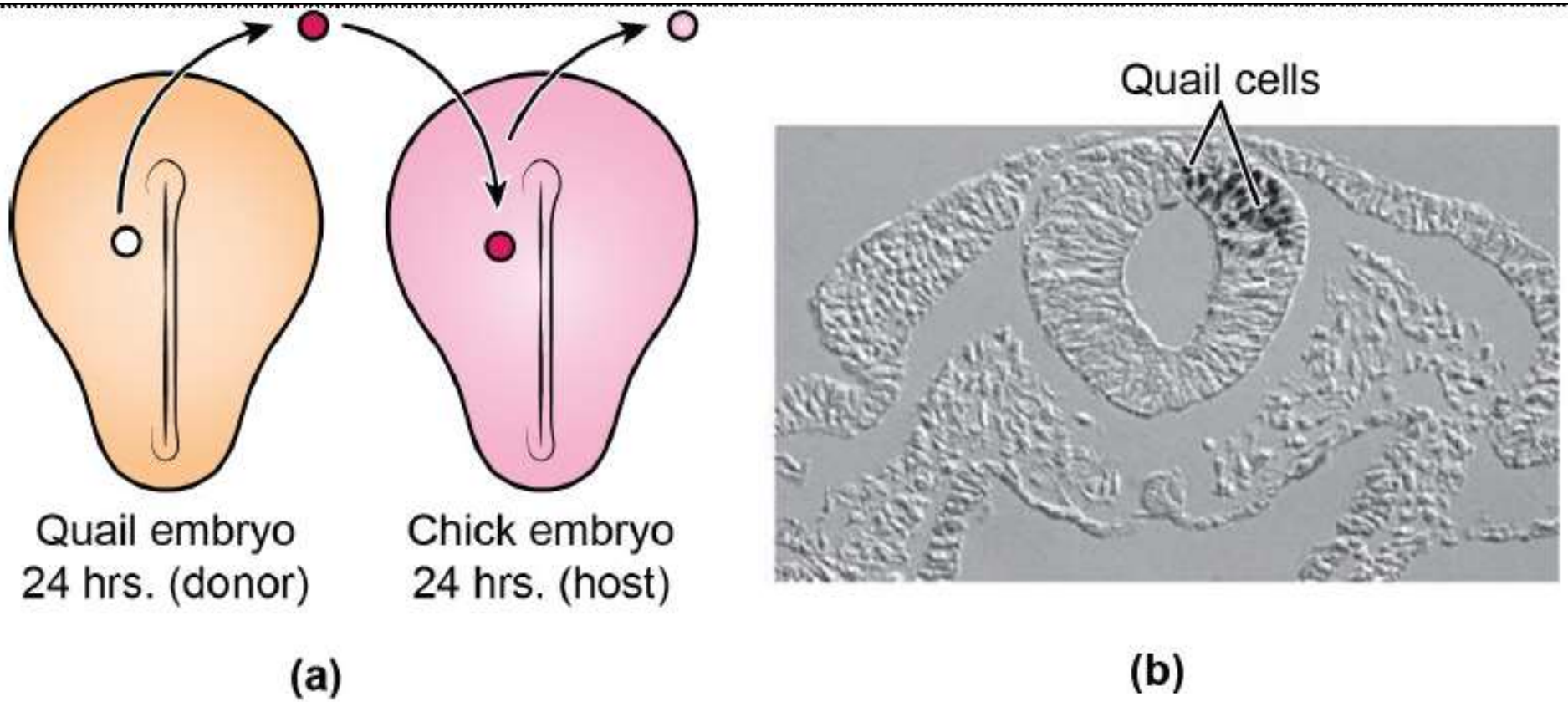

Fig.10.12: Genetic labelling of cells of the living embryos for determining their fate and for constructing the fate map. Cells from the quail embryo are transplanted on chick embryo. As the chick embryo develops the quail cells can be traced in it.

Fluorescent antibody: have been used to study development in the transparent, free living nematode (roundworm) *Caenorhabditis elegans. C.* elegans has been used as a model organism to follow cell lineage from zygote to the adult form under the light microscope by using a fluorescent antibody which is specific for the nematode. The intestine develops from the cells that arise exclusively from one of the four cells that are formed from the first cleavage furrow in the zygote. Other methods that have been used for constructing fate maps, was by destroying particular cells or cell groups by means of a laser beam. Subsequently, the complete fate map and cell lineage of *C. elegans* has been worked out.

The fate map of *Drosophila melanogaster* has also been studied extensively and has revealed the molecular and genetic mechanisms involved in body segmentation and axis formation (Fig.10.13)

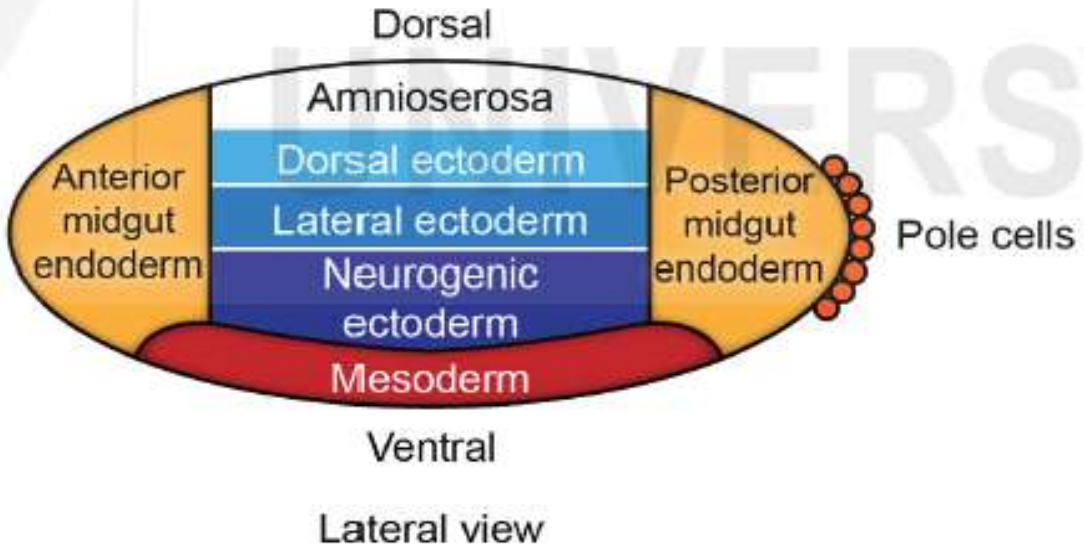

Fig.10.13: Fate map of *Drosophila melanogaster* showing the regions from where the future body tissues and organs will arise. (modified from