GASTRULATION

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13.3 GASTRULATION

The end of cleavage of the zygote results in the formation of a blastula, which in different species could be, a solid structure without a cavity or its cells may be arranged in the form of a one cell or several cells thick epithelium around a cavity or around or on top of the yolk. In any case the blastula has no resemblances to the shape or organization of the body. Therefore, through the subsequent developmental stage, the simple blastula would transform itself into a more complex embryonic structure upon which the adult like body may be built up. Such a process of transformation is known as **gastrulation**. It is a very significant phase of embryological development, which marks the beginning of the form and organization of the adult body.

During gastrulation there occurs displacement of the parts of blastoderm which gives rise to three germinal layers viz. ectoderm, mesoderm and endoderm from which all the future organs will develop. The presumptive endodermal and mesodermal cells move from the surface of blastula into the interior of the embryo where the respective organs are formed during the course of further development. The cells of the presumptive ectoderm remain on the surface. With the exception of some parasitic flatworms a new cavity called the archenteron (future alimentary canal) is formed which is surrounded by endoderm and which thus, initiates the tube within tube structure of the triploblastic animals.

Thus, gastrulation is a dynamic process involving large scale movement of blastula cells resulting in their arrangement in a way which establishes the basic body plan according to which the embryo has to develop further. Since these movements lay the foundation for the form and organization of the body they are called **morphogenetic movements**. These involve the movements of the epithelial cells layers as a whole as well as the independent movements of the cells which break loose from epithelium and become mesenchymal. **In**

In general gastrulation results in the following outcomes:

- The formation of the three germ layers namely ectoderm, mesoderm and endoderm.
- The formation of the embryonic gut or archenteron
- The appearance of the major body axes. Though in some animals the information specifying the body axes is already present in egg in the form of cytoplasmic determinants and or the polarity of the yolk. However, the polarity becomes actually visible during gastrulation.
- Rearrangement of cells of the embryo by means of morphogenetic movements.
- The rhythm of cell divisions slows down. Growth, if any, is insignificant.
- There is intensification of the process of oxidation in the cells.
- The nuclei become more active in controlling the activities of the embryonic cells. The influence of paternal genes becomes evident during gastrulation.
- Proteins of many new types that were not present in the egg or blastula begin to be synthesized.

13.3.2 Morphogenetic Movements

When you look at fate maps it becomes clear why the cells have to move during gastrulation. For example, if you look at the amphibian fate map you can see the presumptive ectoderm, endoderm and mesoderm all as adjacent areas in an epithelial sheet (Fig.13.14). The endoderm and mesoderm must move inside the embryo. Endoderm and mesoderm will separate from the ectoderm and move onside to form the internal gut. Gastrulation is thus a dynamic process involving a variety of coordinated movements of cells of different areas of the blastula. **The movement of cells in the embryo from one place to another to form particular structures is known as morphogenetic movements**.

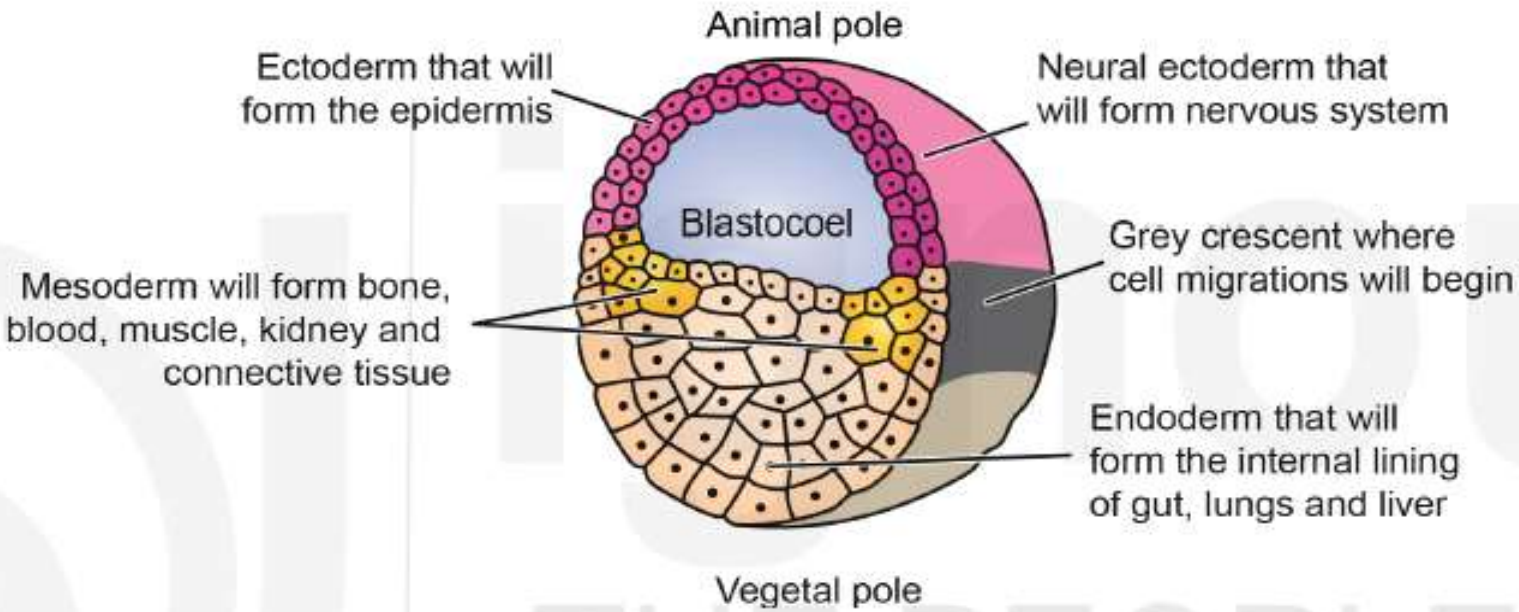

Fig.13.14: Fate map of Frog embryo to show the presumptive ectoderm, endoderm and mesoderm.

In the embryo the morphogenetic movements of cells from one place to another in order to establish a particular form or structural arrangement, occurs during embryonic development from the beginning of gastrulation onwards as well as in the adult body.

In Unit 11 you had learnt that the primary force for morphogenetic movements is provided by cell shape change, cell adhesion, ability of individual cells to migrate. For convenience, the types of cell movements are described separately but it should be understood that two or more of them may occur simultaneously. Broadly, there are two groups of morphogenetic movements in embryonic development i.e., epiboly and emboly.

i) **Epiboly**

Epiboly means to throw on or to extend upon (Fig.13.15). It is the movement of epidermal cell sheets spreading over as a unit to cover the deeper layers of the embryo. It occurs only in the presumptive ectodermal layers (epidermal and neural areas). The cells of this area have an inherent property of flattening, expanding and stretching. The cells of the presumptive ectodermal areas remain on the surface, eventually forming the outer layer covering the entire embryo and enveloping the inwardly migrating presumptive mesodermal and endodermal layers.

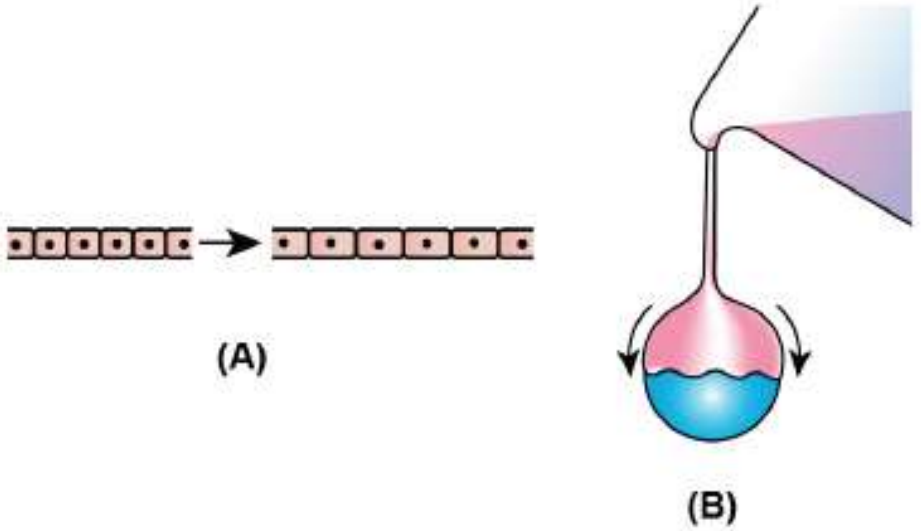

Fig.13.15: A) Epiboly: During epiboly, a sheet of cells spreads by thinning while its overall surface area increases in the other two directions. Epiboly can involve a monolayer (i.e. a sheet of cells which is one cell layer thick), in which case the individual cells must undergo a change in shape. In other cases, however, a sheet that has several cell layers can become thin by changes in position of its cells. In this case, epiboly occurs via intercalation. B) Diagram showing the analogy with epiboly in which a viscous liquid is poured over a sphere. The liquid slowly spreads covering the surface of the sphere.

ii) **Emboly**

Emboly means to throw in or to thrust in. Such movements bring about the migration of presumptive mesodermal and endodermal cells from the external surface of the embryo into its interior.

Emboly includes several different types of cell movements which are as follows:

a) **Invagination**

Invagination specifically includes the process of infolding or rolling in of the presumptive endodermal areas (Fig.13.16) and is the most widely observed embolic movement during gastrulation in most animals, e.g. echinoderms, *Amphioxus* and amphibians etc. Invagination may be passive, occurring as a result of the activity of other cells, or active, resulting from the inherent forces within the invaginating cells.

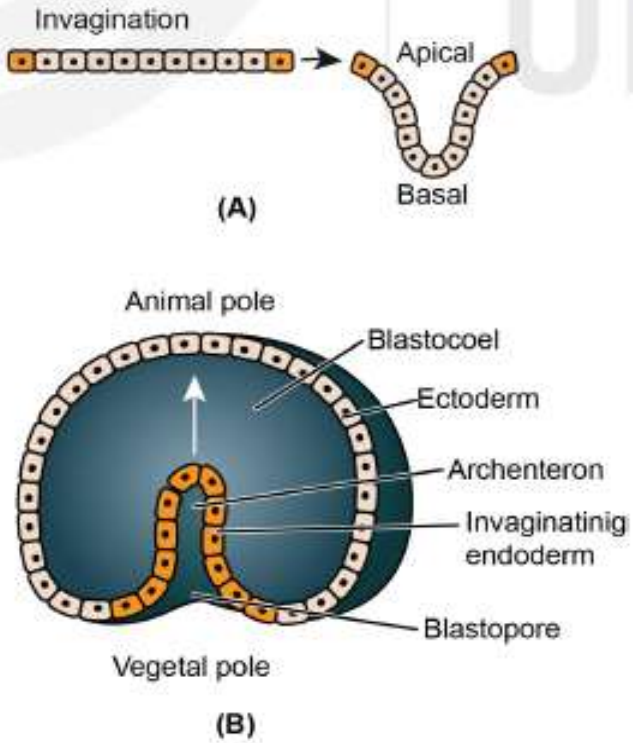

Fig. 13.16: (A) Diagrammatic representation of gastrulation by invagination. During invagination, an epithelial sheet bends inward to form an inpocketing. One way to think of this in three dimension is by imagining that you are poking a partially deflated balloon inwards with your finger. The resulting bulge or tube is an invagination; (B) Gastrula.

Various causes have been attributed to the process of invagination:

- Absorption of blastocoelic fluid by certain cells.
- Differences in the characteristics of blastocoelic fluid and external medium.
- Higher relative alkalinity of blastocoelic fluid which causes local surface tension changes in the membrane of certain cells.

It should be kept in mind that not any one factor causes invagination but a combination of different factors may be involved in various animals.

b) **Involution**

Involution denotes inward movement of an expanding outer layer so that it spreads over the internal surface of the remaining external cells (Fig.13.17). Involution of mesodermal blastomeres has been observed in *Amphioxus,* amphibians, birds, reptiles, monotremes and even in some eutherian mammals.

Fig. 13.17: During involution, a tissue sheet rolls inward to form an underlying layer via bulk movement of tissue. (A) One helpful image here is of a conveyor belt. As the material moves in from the edges of the sheet, material originally at the sites of inward rolling (shown in blue here) is free to move further up underneath the exterior tissue. (B) involution of endoderm in sea urchin.

c) Intercalation

Intercalation is another form of morphogenetic movement. During intercalation, two or more rows of cells move between one another, creating an array of cells that is longer (in one or more dimensions) but thinner. The overall change in shape of the tissue results from cell rearrangement. Intercalation can be a powerful means of expanding a tissue sheet. A specialized form of intercalation is convergent extension (Fig.13.18).

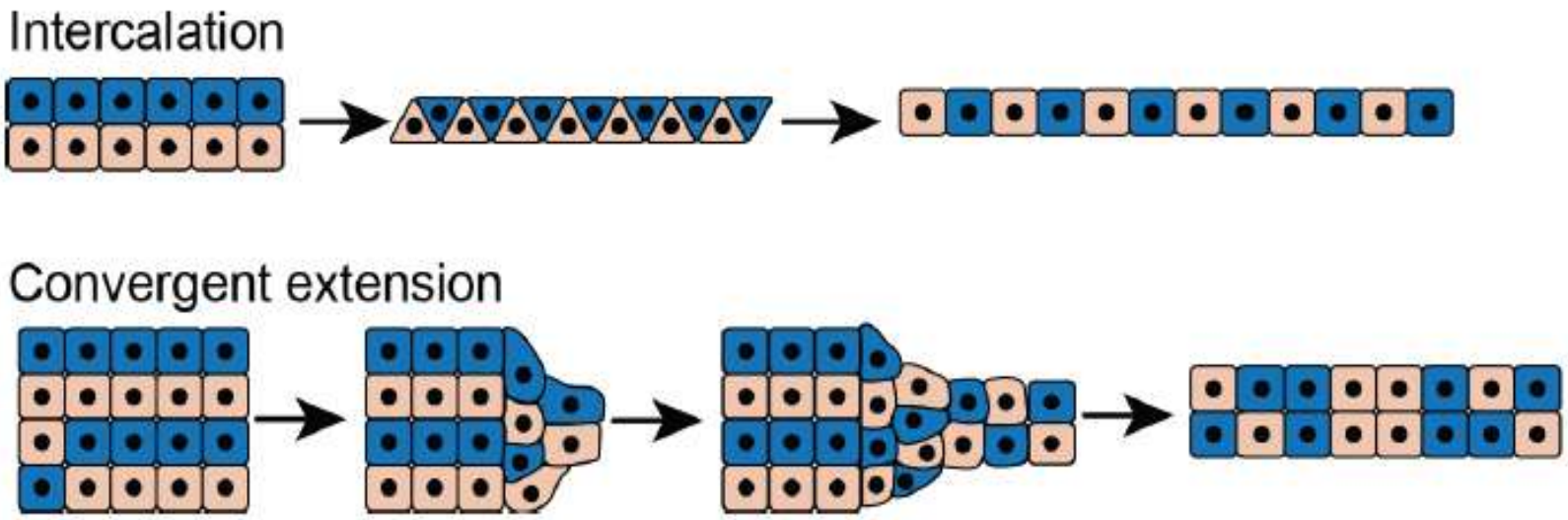

Fig.13.18: Intercalation involves two or more rows of cells that move between one another creating an array of cells.

d) **Delamination**

Delamination (Fig.13.19), denotes the separation of groups of cells from other cell groups to form separate cell layers. It includes splitting of a pre-existing sheet (layer) of cells into two more or less parallel sheets, usually with a space separating them.

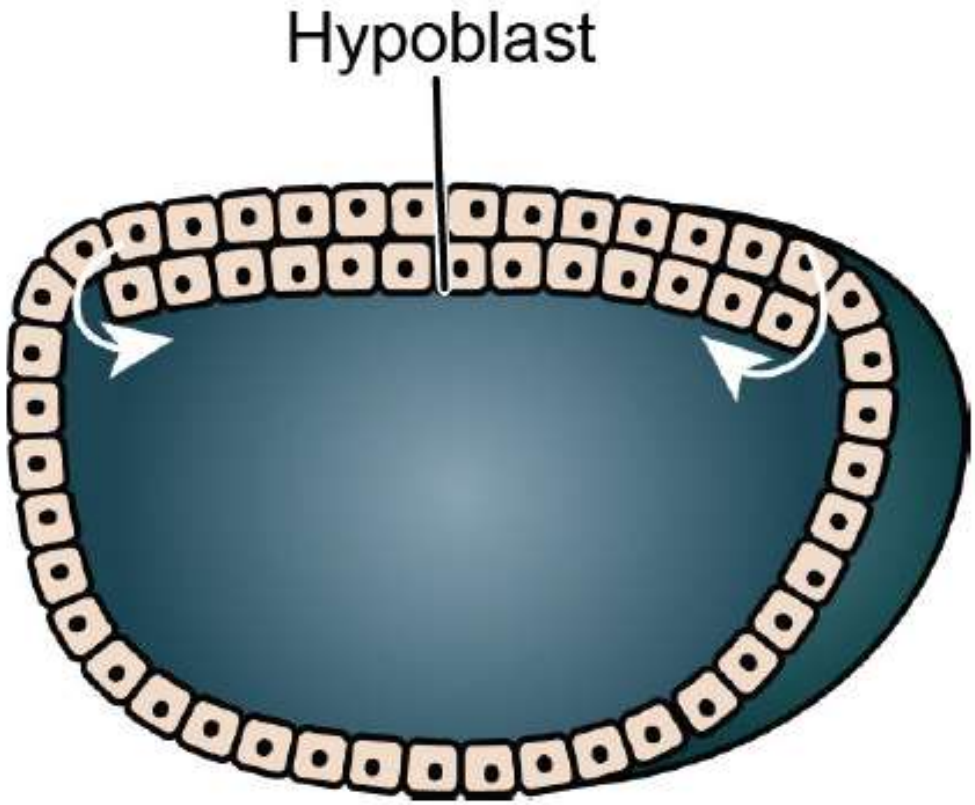

Fig.13.19: Delamination results in the formation of the hypoblast from epiblast in amniotes.

e) **Ingression**

In this process, migration of individual cells from the surface blastoderm or blastodisc into the embryo's interior takes place. Individual cells become mesenchymal (i.e., separate from one another) and migrate independently into the cavity or spaces developed within the embryo (Fig.13.20). Primary mesodermal cells of sea urchin embryo become internal by this process. Neural crest cell are an example of a mesenchymal cell type that emigrates out of an epithelium

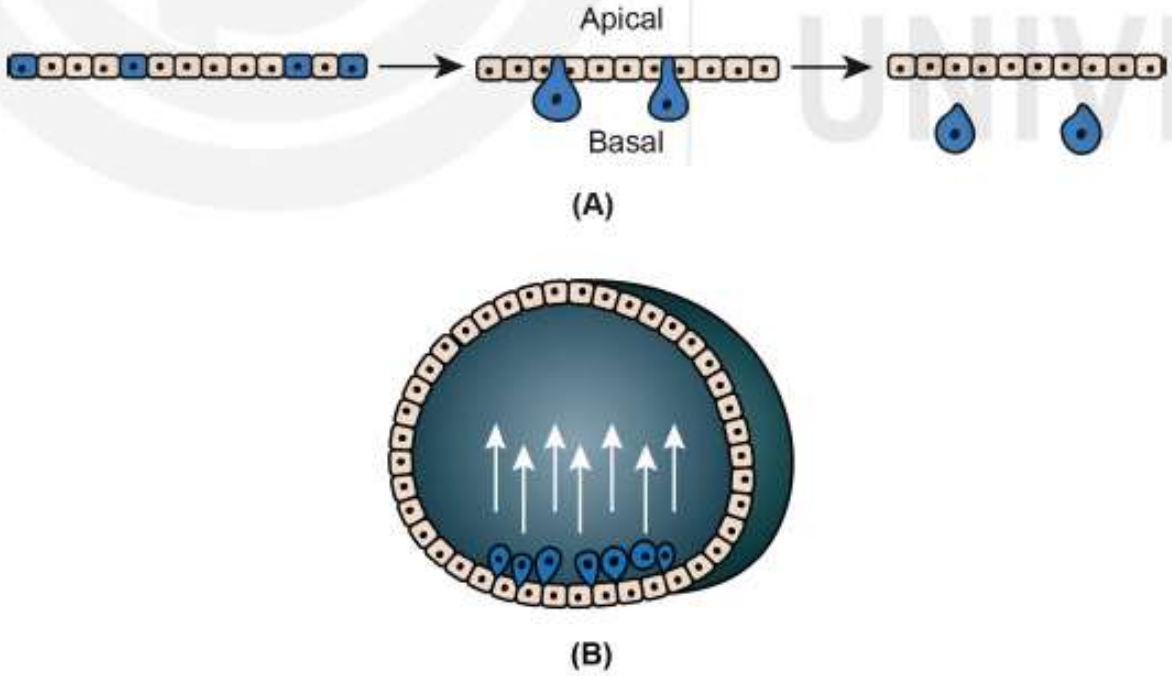

Fig.13.20: Ingression: (A) During ingression, cells leave an epithelial sheet by transforming from typical epithelial cells into freely migrating mesenchyme cells. To do so, they must presumably alter their cellular architecture and their adhesive relationship to the surrounding cells. (B) Diagrammatic representation of ingression of primary mesenchymal cells in sea urchin embryo.