- Initially all the cleavage planes are vertical and so all the blastomeres lie in one plane
- The cleavage furrows separate the daughter blastomeres from each other but not from the yolk.
- The central blastomeres are continuous with the yolk at their lower ends.
- The blstomeres on the circumference are also in contact with the uncleaved cytoplasm an their edges.
- As division continues, more cells are cut off to join the ones lying in the centre, but the new blastomeres are also continuous with the uncleaved yolk underneath.
- The 4th cleavage is circumferential, which separates the central row of cells from the peripheral row of cells
- Later on, the blastomeres of the central row become separated from underlying yolk
- This occurs either by slits that appear beneath the cells or division may occur with horizontal plane of fission
- The cells at the margin remain continuous with each other and the mass of yolk
- All the blastomeres lose their furrows and fuse into a continuous mass with many nuclei but no indication of individual cells

Blastulation

- As the zygote undergoes cleavage, the blastomeres become arranged in a single layer on the external surface of the embryo.
- Scon a cavity appears which increases gradually as cleavage goes on.
- This cavity is called blastocoel.
- The blastomeres adhere to each other and arrange themselves into a true epithelium
- This layer encloses the blastocoel and the embryo becomes a hollow sphere called a blastula.
- In Amphioxus, the blastomeres at the end of cleavage are not of equal size; those at the vegetal pole are slightly larger than those of the animal pole.
- When the blastula is formed, the cells are seen

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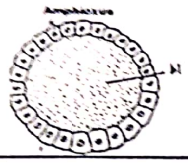
to have arranged themselves into a simple columnar epithelium, enclosing a blastocoel.

- Because of the larger cells in the vegetal hemisphere, the bastoderm i.e the layer of cells is not of equal thickness.
- At the vegetal hemisphere, the epithelium is thicker than at the animal hemisphere
- The polarity of the egg persists in the blastula as well.



small intercellular cavity that is sealed off from the outside by tight intercellular junctions.

- This cavity expands during subsequent cleavages to form the blastocoel.
- The blastocoel serves two major functions in the frog embryo:

1. It permits cell migration during gastrulation.
2. It prevents the cells beneath it from interacting with the cells above it.

- The cells of the blastula show differences in

Blastulation in Amphibians

- An amphibian embryo containing 16-64 cells is commonly called morula.
- At the 128 cell stage, the blastocoel becomes apparent and the embryo is considered a blastula.
- The formation of the blastocoel has been traced back to the very first cleavage furrow
- Kalt (1972) demonstrated that in the frog *Xenopus laevis*, the first cleavage furrow widens in the animal hemisphere to create a

sizes; those at the vegetal pole are much thicker than those of the animal pole.

- Thus the blastocoel is nearer the animal pole of the embryo.
- The frog blastocoel is said to be eccentric.
- It remains in the blastula stage until successive cleavage cycles have increased the cell number to between 10,000 and 15,000 cells.
- The blastoderm is no longer a simple cylindrical epithelium but 2 or more layers thick.

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- The cells in the interior are loosely connected to each other, but at the periphery of the blastula, the cells adhere to each other firmly because of cementing substance joining the surfaces of the cells.
- The amphibian blastula can be subdivided into three main regions:

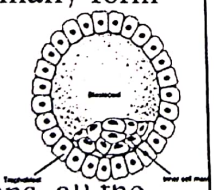
1. A region around the animal pole, including the cells forming the roof of the blastocoel. These cells correspond to the future ectodermal layer.

epithelial layer and only a single layer is formed, but in birds, only some of the blastomeres are incorporated into the superficial layer, the epiblast. Some cells remain beneath the superficial layer.

- These cells lie in the space between the superficial layer and the yolk.
- These cells unite to form a thin flat epithelium called **hypoblast**. This is separated from the surface layer by a cavity. The space between the hypoblast and the yolk is the **subgerminal cavity**

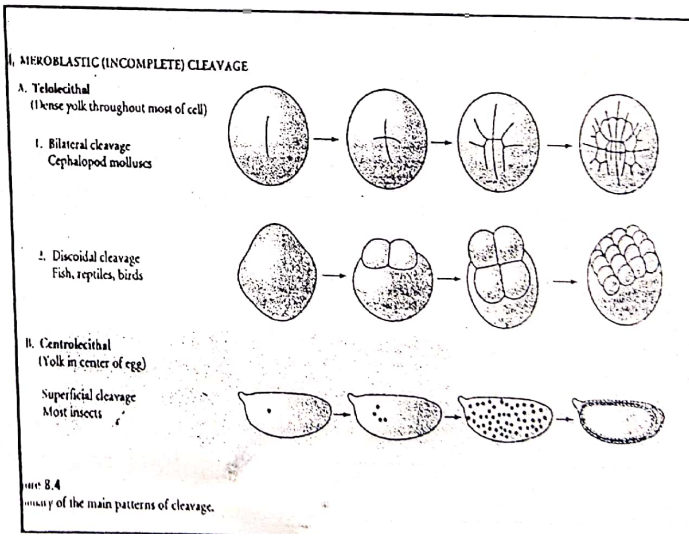
2. A region around the vegetal pole, including he large cells in the interior which constitute the olk mass. These are the future endodermal cells

3. A marginal ring of cells in the subequatorial egion of the embryo, including the region of the grey crescent. Cells of this zone normally form he embryonic mesoderm.



Blastulation in the chick embryo

In some animals such as amphibians, all the blastomeres become converted into an



ure 8.4
mary of the main patterns of cleavage.

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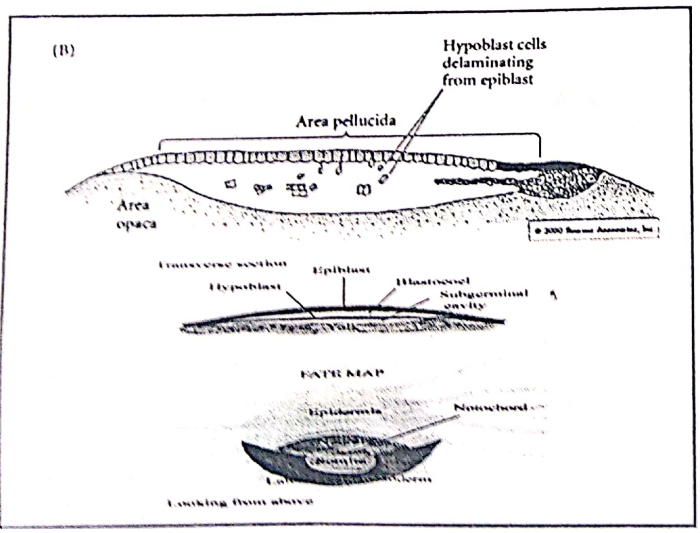
- This cavity does not appear under the whole of the blastoderm but in the central part of it.
- No cavity is formed under the layer of blasomeres in the periphery of the blastodisc.
- The blastodisc is thus subdivided into two parts:
- The central part of it is called the **area pellucida** whilst the peripheral part is the **area opaca**, which is in contact with the yolk.
- Only the area pellucida contains materials for the formation of the embryo.

- The cells of the area opaca break down the yolk to supply the embryo with food.
- The subgerminal cavity cannot be taken as the blastocoel because a blastocoel must have a roof of cells, the epiblast and a floor of cells, the hypoblast.
- If the subgerminal cavity is considered as a blastocoel, it will have an epiblast but no hypoblast since the floor would only be a mass of yolk.
- The mechanism of the formation of the blastocoel involves one of the



following:

- **Delamination**: In this case the cells of the area pellucida, which originally formed the roof of the subgerminal cavity would have a split occurring in them.
- The split widens, separating the cells into the epiblast which forms the roof and the hypoblast which forms the floor.
- Thus in the chick embryo, at the end of blastulation, two cavities are formed;

a) the original subgerminal cavity

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b) the newly formed blastocoel

Theory of involution

- In this case some of the cells of the area pellucida, at the edges boardering the area opaca gets lifted turning downwards and inwards to form a floor, which becomes the hypoblast, with the rest of the cells forming the epiblast. The hypoblast, which ultimately forms the extraembryonic endoderm possesses polarity.
- The two-layered blastoderm of the chick has been compared with the flattened blastula of the frog embryo.
- The epiblast is considered equivalent to the animal hemisphere whilst the hypoblast shares common features with the vegetal hemisphere of the frog embryo.

GASTRULATION

- After cleavage and formation of the blastula, the embryo embarks on one of the most critical periods in its development ie. gastrulation
- Gastrulation is the process of highly coordinated cell and tissue movements whereby the cells of the blastula are dramatically rearranged.
- It also involves the displacement of parts of the early embryo.
- The blastula consists of numerous cells, the positions of which were established during cleavage.
- During gastrulation these cells are given new positions and new neighbours and the multi-layered body plan of the organism is established
- As a result of these movements the cells that will form the endodermal and mesodermal organs are brought to the inside of the embryo, while the cells that will form the skin and nervous system are spread over its outside surface.
- Therefore the three germ layers – outer ectoderm, inner endoderm, and interstitial mesoderm are first formed during gastrulation.

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- Gastrulation involves some combination of the following types of movements:

1. **Invagination.** This is the infolding of a region of cells.
2. **Involution.** The in turning or inward movement of an expanding outer layer so that it spreads over the internal surface of the remaining external cells.
3. **Ingression:** The migration of individual cells from the surface layer into the interior of the embryo.
4. **Delamination:** The splitting of one cellular sheet into two or more parallel sheets. The results is the formation of a new sheet of cells
5. **Epiboly:** The movement of epithelial sheets (usually of ectodermal cells) that spread as a unit, rather than individually, to enclose the deeper layers of the embryo.

- During gastrulation, a number of processes take place:

1. Re-arrangement of cells by means of morphogenetic movements.
2. the rate at which the cells divide is reduced
3. growth becomes insignificant
4. intensification of oxidation
5. the nuclei become active in controlling the activities of the embryonic cells
6. there is the synthesis of new proteins

Fate maps

- It has been shown that specific regions of the early embryo contribute to the formation of different tissues and organs in the adult
- It is possible to stain different parts of the developing zygote with different dyes.

These dyes do not kill the cells and therefore do not arrest the process of development

- As each region is stained it is possible to follow the fate of each region.
- Having followed the fate of several regions , it is possible to construct a fate map i.e project back to the blastula, marking out what each region would ultimately develop into.
- A fate map is a chart showing the fate of each part of an early embryo, particularly a blastula.

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- The different identifiable regions of the fate map are known as the presumptive organ forming areas.****

Gastrulation in Amphioxus

- During gastrulation, the three germ layers of a triploblastic animal are formed.
- Gastrulation in Amphioxus is initiated with the flattening of the cells in the vegetal hemisphere, which subsequently bends inwards, so that the embryo instead of being spherical becomes converted into a cup-like structure.
- The flattened cells begin to push inwards in a process called invagination.
- Invagination continues until a double walled cup is formed; an external and internal wall.
- The internal wall lines the newly formed cavity.
- The external and internal epithelial layers are continuous with each other.
- At this stage there is still a space between the external and internal wall, represented by the remains of the blastocoel.
- As invagination continues the blastocoel becomes smaller until it finally disappear.
- The external lining consists of the presumptive epidermis and presumptive nervous system.
- The internal lining consists of presumptive gut material ie the endoderm.
- The presumptive material of mesoderm and notochord initially lie on the rim of the cup, but soon they shift to occupy a position on the internal wall of the cup.
- The presumptive notochord, mesoderm and endoderm disappear from the surface of the embryo into the interior, where they belong.
- The external surface now consists of the ectoderm.
- The embryo at this stage is called a **gastrula** and the cavity that results after invagination is the primary gut or **archenteron.**
- The opening of the archenteron to the outside is called the blastopore.
- The blastopore also marks the pathway by

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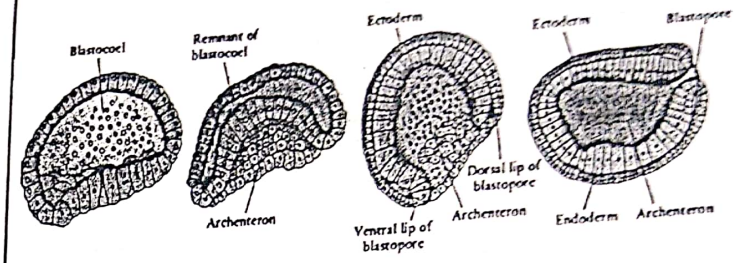
which the cells of the mesoderm and endoderm pass into the interior of the embryo.

- The blastopore, being the opening into the primary gut has been likened to a mouth, its rims are therefore called the lips of the blastopore.
- The blasopore is broad initially, but the lips begin to contract so that the opening becomes smaller.
- When the presumptive notochord and mesoderm shift into the interior of the embryo

Gastrulation in Amphioxus



they change their position relative to each other.

- During gastrulation the embryo rotates so that the future dorsal surface comes to lie uppermost , with the ventral side below.
- There is the stretching of the presumptive organ-forming areas in the anterior-posterior direction to make the embryo elongated.
- This brings mesodermal and notochordal materials closer together.
- The external wall of the gastrula takes part in the elongation of the embryo.
- The presumptive material of the nervous system becomes stretched into a longitudinal band of cells lying over the notochordal material.

Gastrulation in the frog

- Gastrulation in the frog embryo is modified by the large yolky cells in the vegetal hemisphere.
- At the beginning of the process a groove or depression forms at the boundary between the grey crescent and vegetal hemisphere by

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invagination.

- The cells at the bottom begin to stream into the interior of the embryo toward the blastocoel.
- This process marks the beginning of the formation of the blastopore.
- The groove begins to spread transversely; its lateral ends are prolonged along the boundary between the marginal zone and the vegetal region until they meet, thus encircling the vegetal region.

- By the time the blastopore has the form of a ring the cells of the vegetal region fill the space enclosed by the edge of the blastopore.
- The cells form the yolk plug.
- The rim of the blastopore contracts and finally covers the yolk plug.
- Thus the material in the vegetal hemisphere disappear into the interior of the embryo.
- The yolk plug disappear from view and the blastopore is said to be closed.
- During gastrulation the first group of cells to

- In the animal hemisphere the yolk is not much, thus the cells there divide faster than those of the vegetal hemisphere.
- The cells of the animal hemisphere become many and therefore begin to flow down towards the blastopore.
- They converge at the dorsal lip and move inside.
- The process of flowing down of the animal cells and their subsequent involution is known as epiboly.

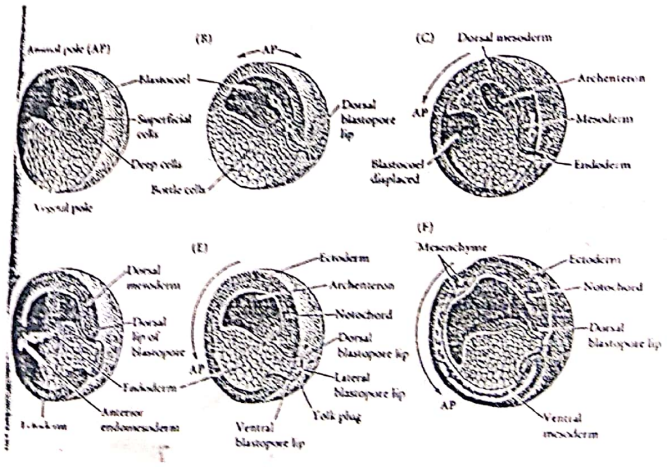

Figure 10.7
Cell movements during frog gastrulation. The meridional pathways are out through the

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...s gastrulation: added complexity but similar mechanisms

2. Involution of Marginal zone cells

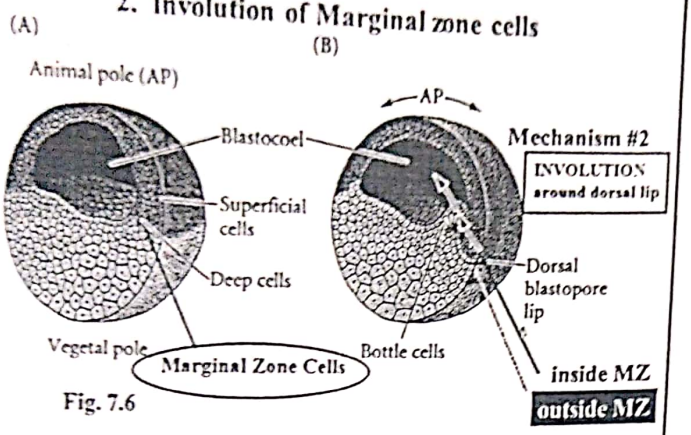

Fig. 7.6

or archenteron.

- After involution the cells move away from the blastopore by a process called **divergence.**
- By the end of gastrulation the blastopore has been reduced to a slit.

The ectoderm

- The material of the animal region, the presumptive epidermis and presumptive nervous system covers the whole of the embryo after the mesoderm and endoderm have moved inside.

reach the blastopore form the dorsal lip.

- Cells of the ventral side also flow towards the blastopore and when they reach, form the ventral lip.
- Some of the cells of the dorsal lip flow down to the sides to form the lateral lips.

Once the blastopore is formed, the cells of the presumptive organ-forming areas roll over and move inside; this is known as involution.

Soon a cavity is formed, beginning from the blastopore, widening to form the gastrocoel

- The presumptive epidermis expands in all directions, but in the case of the presumptive nervous system, the expansion is mainly in the longitudinal direction.
- In the transverse direction the presumptive nervous system contracts.

Notochord: the cells of the notochord roll over the dorsal lip of blastopore into interior of the embryo and becomes stretchered along the dorsal side of the embryo.

- The presumptive notochord undergoes

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elongation in longitudinal direction and contraction in the transverse direction.

- The notochordal material becomes concentrated on the dorsal side of the embryo.
- **Mesoderm:** The mesodermal cells roll over the lateral and ventral lips of the blastopore
- Inside the embryo they arrange themselves between the ectoderm and endoderm.
- **Endoderm:** In the blastula, the presumptive endoderm is partly found in the marginal zone and partly in the vegetal region.

NEURULATION

- Neurulation is the process whereby the neural plate becomes transformed into the dorsal hollow tube, the neural tube.
- The embryo at this stage is called a neurula.
- During this time, the primordia of the brain, spinal cord and neural crest become internalized and completely segregated from the rest of the surface ectoderm.
- The future development of the embryo depends on the inductive interactions between

- Cells in the vegetal region become covered by the contracting rim of the blastopore.
- The endodermal cells at the bottom are later found in the duodenal region of the embryo.
- The endoderm of the vegetal region passes into the interior and comes to lie in the floor of the archenteron.
- This layer of endoderm is very thick, reducing the cavity of the archenteron.
- This narrow part of the archenteron forms the mid-gut of the embryo.

some of these newly associated groups of cells.

- The primary inductive event is the action of the chordamesoderm or notochord on the overlying ectoderm, resulting in the transformation of a band of unspecialized cells into the primordium of the central nervous system.
- The initial response of the induced ectoderm is to form a plate of thickened cells, but soon after this the plate becomes transformed into a longitudinal groove and finally into a plate.

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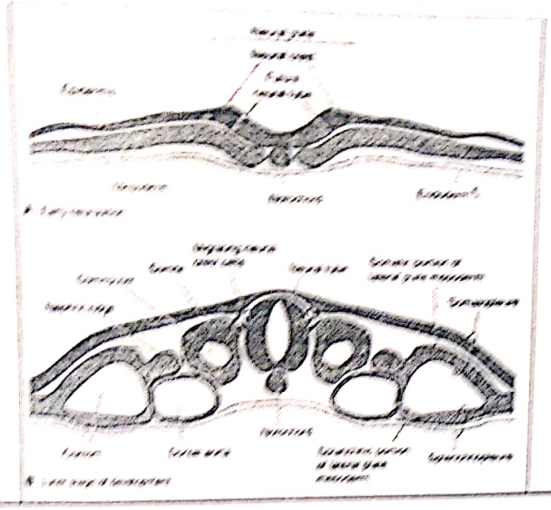
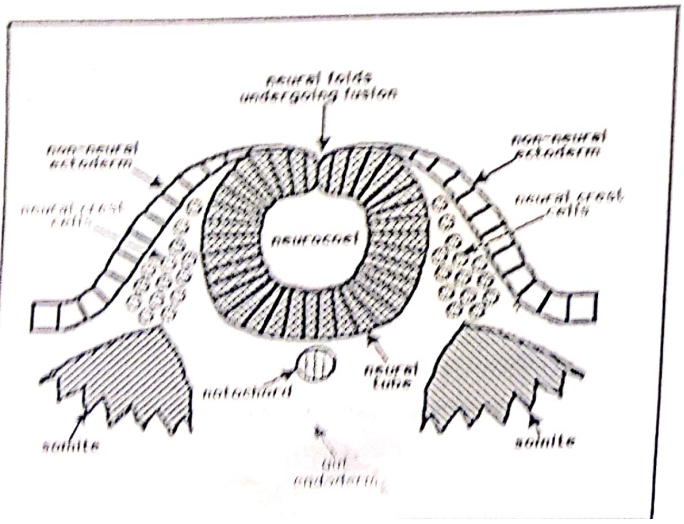


Primary (neural) Induction

- During late gastrulation, the chordamesoderm pushes cranially just beneath the ectoderm.
- While the forward movement of the notochordal tissue is taking place, the notochordal cells act on the overlying ectodermal cells, causing them to thicken to form the neural plate.
- This reaction, which initiates the formation of the central nervous system, causing the central longitudinal axis of the body to be established



is called primary induction.

- The inducer or inductor is the chordamesoderm and the responding tissue is the ectoderm.
- Like other inductive systems, it is essential that the inductor and responding tissue be at the right place at the right time.
- Without the presence of the underlying notochord, the cells of the dorsal ectoderm do not form neural tissue but rather continue to differentiate as general cutaneous ectoderm.

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- In order for neural induction to occur, the ectoderm overlying the notochordal process must be able to respond to the inductive stimulus, i.e. it must be competent.
- During much of the period of gastrulation in the amphibian embryos, both the dorsal and ventral ectoderm have the competence to form neural tissue when subjected to the influence of inductors.
- Later in gastrulation the ectoderm farthest from the normal location of nervous tissue begin to lose their capacity to respond to neural inductors, and late in the neurula stage most non-neural ectoderm lose their competence.
- Following changes leading to the formation of the neural tube, the mesoderm on either side of the notochord splits into longitudinal divisions.
- The blocks of mesoderm on either side of the notochord begin to form symmetrical pairs of brick-like masses called somites.

- A number of processes are important in the morphogenesis of thin layer of cells.

1. **Epithelial folding** this is usually preceded by elongation of cells in a direction perpendicular to the exposed surface, a process called palisading.
- When the folding is inward from the free surface it is called **invagination**.
- When the folding is outward from the surface or lumen, it is called **evagination**.

2. Detachment of cells from each other.

Epithelial layers or cell mass may be subdivided into parts by the appearance of gaps/crevices between groups of cells.
- The cells on the opposite sides of the crevice lose connection with one another.
- The original crevice may be increased by the secretion of fluid into it, becoming a spacious cavity.

3. Thickening of epithelial layer
- A very common method of organ formation
- The thickening is brought about by the

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epithelial layer flowing toward the region where the organ is to appear.

- For example, in the formation of the neural plate, the epithelial thickening is towards the mid-dorsal region of the embryo.

4. **Fusion of previously separated parts**

- This plays a critical role in morphogenesis
- For example, the edges of the neural folds fuse along the dorsal midline to form the neural plate.

5. Breaking up of epithelial layers to produce

of the primitive gut.

- The blastopore decreases in size and finally closes.
- During the latter stages of gastrulation the process of primary induction is coming to an end and the ectoderm which overlies the notochord has begun to respond by thickening to form the neural plate.
- The neural plate assumes the shape of a key hole, being wider at the anterior end where the future brain will develop.

mesenchyme: This process makes materials available for the development of organ rudiments.

- In this case an epithelial layer or a portion of it may break up into mesenchyme so that the epithelium disappears, or a gap is left in the previously continuous layer eg the formation of the neural crest.

Neurulation in the Frog

- The latter stages of gastrulation are dominated by cell movements that lead to the formation

- The margins of the neural plate then becomes thickened and raised to form the neural folds
- The neural folds then converge in the dorsal midline and fuse to form the neural tube.
- At the same time as the neural folds meet each other , the embryo elongates along the anterior-posterior axis.
- In the interior of the embryo, the primitive gut becomes surrounded by endodermal cells.
- Surrounding the endoderm is a complete layer of mesoderm.

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- The notochord at this stage is a discrete rod in the dorsal mid-line.
- On either side of the notochord, the dorsal part of the mesodermal sheet (epimere) thickens and undergoes segmentation.
- The paired mesodermal segments later become the somites.
- The broad mass of early mesoderm(hypomere) located on the lateral and ventral parts of the embryo is called the lateral plate mesoderm.
- Later on the lateral plate mesoderm splits into two layers: an outer layer attached to the ectoderm (parietal or somatic mesoderm) and an inner layer surrounding the endoderm known as visceral or splanchnic mesoderm
- The somatic mesoderm and the overlying ectoderm are collectively called the somatopleure.
- The splanchnic mesoderm and the underlying endodern are collectively called splanchnopleure.
- The cavity that forms between the 2 layers of mesodermal cells is known as the coelom

Neural crest

- After the formation of the neural tube, it detaches itself from the overlying epidermis.
- There remains a group of cells that do not form part of the neural tube or epidermis.
- These cells are the neural crest cells.
- Initially the neural crest cells may be continuous across the midline, but later the mass of cells separate into the left and right halves.
- The neural crest cells have the ability to migrate throughout the body.
- In the head region the cells of the neural crest migrate as a unit, whereas in the trunk the cells move individually.
- The cells leave the neural crest in 2 streams:
- One group is superficially and dorsally directed; the other is ventrally directed.
- Cells that follow the dorsal pathway move into the ectoderm, differentiate into pigment cells and settle either in the epidermis or dermis.
- Cells that move ventrally develop into some

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components of the nervous system.

- Other cells remain close to the original neural crest but become aggregated into dorsal root ganglia of the sensory nerves.
- Cells from the cranial region of the neural crest form much of the musculature and connective tissue of the face.

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