# Chapter 1 Comparative Embryology

**Objective:** To acquaint the learner with key concepts of embryology.

**Desired Outcomes**: Learner will be able to understand and compare the different pre-embryology stages. Learner will be able to appreciate the functional aspects of extra embryonic members and classify the different types of placentae.

**Introduction:**

Like growth, metabolism and irritability, reproduction is one of the properties of the living organisms. Reproduction is the process of multiplication in individuals in the population belonging to a species. It ensures the from and function of an organism. Animals have adapted for the multiplication and their survival with the process of reproduction. Reproduction is basically classified as asexual and sexual types. The sexual reproduction involves gametogenesis (formation of sex cells or gametes like sperms and ova in germinal epithelium of testis and ovary respectively), fusion of gametes (fertilization), egg formation and the embryonic development (zygote transformation). Development of embryo plays very important role in reproduction. Also, it is known that the embryonic development plays important role to know the

evolutionary tract of the species (ontogeny repeats the phylogeny). Based on the embryonic evidences' animals are classified into protostomes and deuterostomes. Protostomes are inclusive of invertebrates which develop mouth from blastopore (poriferans to molluscans) whilst the deuterostomes develop mouth opposite to blastopore by forming separate opening and blastopore develops into anus (echinoderms onwards). The higher vertebrates are further classified into anamniotes and amniotes as they do not or do have the extraembryonic membrane known as amnion respectively.

## 1.1 Types of Eggs: Based on Amount and Distribution of Yolk

The primitive aquatic has adapted to reproduce in aquatic medium which is best suited for their embryonic developments in due course of evolution. With the evolution the higher forms, like amniotes (reptiles, birds and mammals), have adapted to live in dry terrestrial environment. However, in terrestrial animals, who have internal fertilization but the external development to embryo (outside the body of mother), their ova get transformed into shelled eggs which carry huge amount of yolk. In placement animals to yolk is present in negligible amount since the embryo in nurtured through feto-maternal association of tissue called placenta. Although yolk is an essential food reservoir playing important role in development of the embryo, it has been observed that it causes the polarity in the egg and hinders the development of embryo. The area of heavy deposition of yolk is there known as vegetal pole and on opposite side with nucleus and concentrated cytoplasm is known as animal pole

**(Fig 1.1). The animal pole inside the egg is vital end where metabolism takes place for the embryonic development.**

**Figure: 1.1 A schematic diagram showing animal and vegetal poles of polarized egg of frog.**

Dependent on the adaptive radiation, animal have developed various methods of reproduction. The development of ova egg is not an exception. The ova and eggs, by and large, are commonly referred as 'eggs' and are classified into categories further based on the amount and allocation of yolk within the egg.

**Figure: 1.2 Classification of eggs on the bases of amount and distribution of yolk.**

### 1.1.1. Classification of eggs based on amount of yolk

Based on the amount of yolk present, the eggs are classified into two groups as oligolecithal and polylecithal eggs which are further subdivided into alecithal, microlecithal, mesolecithal and macrolecithal (megalecithal) respectively.

**A. Oligolecithal Eggs:**

Oligolecithal eggs contain negligible amount of yolk and hence they are not capable of complete development of embryo and are subjected to undergo several metamorphic stage like larvae, pupae and instars (invertebrates) or they acquire the support of mother by forming placenta ( mammals) for further development.

These types of eggs undergo holoblastic cleavage since there is no hindrance due to yolk.

**i. Alecithal Egg**

Alecithal egg is characterized its negligible amount of yolk. In such a case the embryo needs to be implanted immediately after fertilization to from placenta. Placenta is a union of maternal and foetal tissues formed inside the uterus of mother for the exchanges of gases and nutrients so as to execute complete development of the embryo e.g. Eutherians ( placental mammals)

**ii. Microlecithal Egg**

This type of egg contains very little and mostly evenly distributed yolk. E.g. insects, Amphioxus and tunicates. Therefore in insects the development is indirect and embryo undergoes stages of development like which is allowed to feed extensively to acquire the energy essential for its further development known as metamorphosis. Tunicates also form a short living tadpole larva before developing into an adult. While in Amphioxus the development undergoes rapidly to cope with the meager yolk reserve in the egg.

**B. Polylecithal Eggs:**

Generally oviparous animals produced polylecithal eg. These eggs are havily laden with yolk enough for the complete development of the embryo before hatching. They are further classified as mesolecithal and macrolecithal types.

i. **Mesolecithal Egg**

   This type of egg contains moderate amount of yolk which is largely confined to vegetal pole. Animal pole has cytoplasm and nucleus. The mesolecithal eggs undergo holoblastic cleavage but comparatively slower, particularly in vegetal pole, than that of mocrolecithal eggs e.g. Petromyzon, Dipnoi (laugfish) and amphibiasn.

ii. **Macrolecithal Egg**

   Macrolecithal or megalecithal egg contains large amount of yolk. Terrestrial animals like reptiles, birds and some mammals lay eggs with huge amount of yolk. This ensures a complete growth of embryo inside the egg itself before it hatches out. Due to the large amount of yolk the cleavage is of meroblastic type e.g. bony fishes, amphibians, reptiles and bird and monotremes (egg laying mammals)

**1.1.2. Classification of eggs based on distribution of yolk**

As the egg of animal store different amount of yolk, there is a variation in its distribution in the egg proper. Microlecithal eggs show even distribution of the yolk while in the macrolecithal eggs it many be pushed to one end. Depending upon the distribution of yolk, the eggs are classified as isolecithal, telolecithal and centrolecithal.

**A. Isolecithal or homolecithal Egg**

Isolecithal eggs contain very little amount of yolk which is distributed uniformly in the cytoplasm. These eggs undergo holoblastic cleavage e.g. echinoderms, Amphioxus, mammals etc.

**B. Telolecithal Egg**

The eccentric distribution of yolk defines them as telolecithal eggs. These eggs contain very high amount of yolk usually concentrated at the vegetal pole. Therefore the telolecithal eggs show pronounced polarity. The vegetal pole is large and prominent in telolecithal eggs; hence cleavage is of meroblastic type (partial). These eggs are further sub-divided as slightly telolecithal, moderately telolecithal or pronounced telolecithal type.

i. **Slightly telolecithal egg:** It has small quantity of yolk which is distributed unevenly. The vegetal hemisphere has the highest concentration and the animal hemisphere the lowest e.g. eggs of fishes. In the case nucleus is placed in the center. e.g. eggs of fishes

ii. Moderately telolecithal egg: It contains a moderate quantity of yolk which is distributed unevenly. Due to high concentration of yolk in the vegetal hemisphere, the nucleus is shifted more towards the animal hemisphere e.g. egg of amphibian.

iii. Pronounced telolecithal egg: In the type of egg, due to the heavy deposition of yolk, the entire vegetal hemisphere and a major portion of the animal hemisphere is occupied by yolk. Due to this extremely uneven distribution of yolk, the ooplasm and nucleus are displaced towards the animal pole e.g. of reptiles and birds.

**C. Centrolecithal Egg**

The centre of the eggs is occupied by nucleus and a small amount of cytoplasm which is covered by a thick layer of yok. At the periphery the yolk is a thin layer of cytoplasm which is connected by fine strands of cytoplasm to central vital part e.g. arthropods and some coelenterates.

Fig: Classification of eggs bsed on amount of yolk

1. Alecithal egg
2. Microlecithal egg
3. Mesolecithal egg
4. Macrolecithal egg

Classification of eggs based in distribution of yolk

Isolocithal egg

Telolecthail egg

Centrolecithal egg

Fig: 1.3: Diagrammatic representative of classification pf eggs on the bases of amount and distribution of yolk.

### 1.1.3. Mosaic and regulative eggs:

A. Mosaic or Determinate Egg: Every part to be developed of the future embryo is predetermined in egg itself before or at the time of fertilization. If any position is removed from the egg then the related organ does not develop in that embryo. Such an egg is called mosaic or determinate egg e.g. Polychaete, Nimertine, Annelids, Molluscs and Ascidians.

B. **Regulative or Indeterminate Egg**: The eggs in which developmental potentialities for different organs of future embryo are not predetermined, are referred to as indeterminate eggs. In regulative eggs the determination occurs only third cleavage. If the blastomere of such an egg is removed before the third cleavage, it develops into a complete embryo. In humans identical twins develop due to such an attribute of the egg.

   Eggs are either shelled or non-shelled. The animals which lay eggs on dry land, develop calcareous shell are known as cleidoic egg e.g. reptiles and birds and the animals which exhibit internal development of the embryo, lay their eggs without the shell, such eggs are referred as non-cleidoic eggs e.g. mammals.

## 1.2 Structure and Types of Sperms

Sperms or spermatozoa (singular: spermatozoon) are produced by the germinal epithelium of seminiferous tubules by the process of spermatogenesis. Sperm is a means of transport of genetic material from male to the oocyte of a female. It carries haploid set of chromosomes. It is short lived active gamete which has to find the egg for fusion within a minute most of the time or else they perish.

The mature sperm cell is slender; in the middle part, the mitochondria are thick and ring-shaped. The DNA in the nucleus is maximally condensed.

Figure 1.4: Structure of sperm

### 1.2.1 Basic structure of sperm

Although the structure of sperm varies from species to species, it is singnificantly similar in vertebrates. The structure of a typical mammalian sperm is basically differentiated into head, neck and tail. Tail is further differentiated into mid-piece, principle piece and end piece.

**Head of spermatozoon**

Head is the anterior most part of sperm and is made of a cap-like acrosome and nucleus.

**Acrosome**

The anterior end of sperm head is a crescentic, cap-like structure called acrosome. The shape and size of the acrosome vary among different species. The acrosome enveloped by an acrosomal membrane and it contains certain acrosomal polysaccharids viz. galactose, mannose, fructose, and hexosamine and many enzymes, especially hydrolses. It also contains two proteolytic enzymes (called as hyaluronidase and acrosin) which help in the entry of sperm into the ovum during fertilization.

**Nucleus**

The nucleus of the sperm occupies major part of the head. It comprise of DNA and nuclear proteins and thus is responsible for the transmission of hereditary characters

**Neck**

Neck is a constricted junction between the head and mid-piece. It carries anterior proximal centriole and the posterior distal centriole. The distal centriole gives rise to central axial filaments called axoneme made of microtubules to support the tail region which is used for locomotion. Neck also contains two or three mitochondria and which lie in continuation with anterior mitochondria of mid-piece.

**Tail of spermatozoon**

Tail or flagellum is the locomotory organelle of sperm and its length is approximately three fourth the total length of the sperm. It has three parts viz. mid-piece, principle piece and end piece. The sperm moves in a fluid medium inside the female genital tract by the undulating movement of the tail.

**Mid-piece**

Mid-piece lies between neck and principle piece of tail. It is made of an axial filament surrounded by helix of mitochondria and little amount of cytoplasm. Mitochondria

**Principle piece**

It is the second part of the tail consisting of the axoneme having microtubules arranged as 9 doublets peripherally and 2 single ones in the center (typical 9+2 arrangement of an axoneme). Surrounding this arrangement of microtubules is a sheath made of nine ring fibres. The fibrous sheath terminates at the commencement of the end piece.

**End piece**

The end piece has axoneme extending in it but is without fibrous sheath. The number of microtubules is reduced merely to a pair of single microtubules at its terminal end.

**1.2.2. Types of sperms in animal**

The structure of sperm varies in both invertebrates and vertebrates. The size of sperm ranges from 0.018 mm in Amphioxus to as large as 2.25 mm in toad. The shape of the head also varies from species to species. It is branched or star-shaped in crustaceans and salamander; spherical in teleosts; lance-shaped in amphibians and domestic fowl; hook-shaped in mouse and rat; spoon shaped in several mammals including man.

Furthermore, the sperm may be flagellate or non-flagellate (Ascaris and some crustaceans). Flagellate sperms may be uniflagellate having a single flagellum (many animals), biflagellate having two flagella (toad fish and flatworm) and multiflagellate having many flagellae (some crustaceans and cladocerans). In uniflagellate sperms the head differ in shape according to species e.g. rat sickle

Shaped, amphioxus, bull, rabbit, horse and humans have club shaped whereas domestic fowl has lancet shaped head of the sperm.

Figure 1.5 Types of sperms in animal

**1.2 Types of Cleavage-Holoblastic and Meroblastic Cleavage**

Fertilized egg is a single-cell structure which rise to a multi-cellular embryo through the process of cleavage. During cleavage, the zygote divides repeatedly by mitosis into progressively smaller cells called blastomeres. Cleavage in characterized by rapid and successive mitotic divisions without nay intervening periods of growth. Therefore, blastomeres do not increase in size and the resulting blastomeres are only half the original size. Thus, cleavage begins with one very large cell and with large number of smaller cells. Furthermore, since there is no growth in the size of the blastomeres, the total size and volume of the embryo remains the same. The ratio of nucleus to cytoplasm is very low at the beginning of cleavage, but at the end of cleavage (blastula stage); it is brought to the level found in ordinary somatic cells. Early cleavage divisions occure synchronously i.e. all blastomeres present divide simultaneously and result in the blastomeres have been formed and c cavity appears which is called blastocoel. The resulting multicellular structure (embryo) formed as a result of cleavage is called the blastula.

The various planes of cleavage arise according to a fairly definite pattern and in a particular relationship to each other. Cells typically tend to divided into equal parts (daughter cells). Each new plane of division tends to intersect the previous plane at right angles. This helps to maintain the spheroidal shaped of the blastomeres. The first cleavage division is often along the polar (animal-vegetal pole) axis of the egg called the first meridional cleavage. The second division is also vertical and takes place at right angle to the first cleavage. Thus, both the first and second mitotic divisions are meridional and at right angles to each other. The plane of third division is horizontal and either at /slightly above the equator.

Cleavage is influenced by the quantity of yolk and also the pattern of distribution of yolk in the egg. This is because yolk is an inert material and it hinders the progress of cleavage furrows. The division takes place faster at the animal hemisphere and is relatively slow at the vegetal hemisphere. In fact, if the yolk is in large amount then the division (cleavage furrows) may be incomplete. Thus, cleavage occurs more readily in the active cytoplasm (yolk-free) rather than the yolk-laden cytoplasm (deutroplasm) of the egg and is therefore classified into Holoblastic and Meroblastic cleavage types based on whether the cleavage is total or partial. In placental mammals (including humans) where nourishment is provided by the mother's body, the eggs have a very small amount of yolk and undergo holoblastic cleavage. Other species, such as birds, with a lot of yolk in the egg to nourish the embryo during development, undergo meroblastic cleavage.

**1.1.4 Holoblastic cleavage**

Holoblastic cleavage means complete division and blastomeres stand distinctly separate from each other. It is possible only when egg contains small or moderate amount of yolk deposit e.g. microlecithal (isolecithal) egg and mesolecithal egg respectively. The holoblastic cleavage can be defined into two major types depending upon the size of blastomeres viz. equal holoblastic cleavage and unequal holoblastic cleavage. The equal holoblastic cleavage gives rise to equal sized daughter cells. Whereas in unequal holoblastic cleavage the blastomeres are of unequal size, the ones which develop in animal hemisphere are smaller compared to those in vegetal pole. In vegetal hemisphere the blastomeres formed are of bigger size as they develop slowly due to deposition of yolk. The holoblastic cleavage is further categorized into four major types based on the symmetry viz. bilateral holoblastic, radial holoblastic, spiral holoblastic, cleavage and rotational holoblastic.

When the cleavages furrow divides the egg or blastomeres completely, it is called holoblastic cleavage. The entire egg divides completely into many blastomeres yolk.

Holoblastic cleavage further classified into equal and unequal.

**i. Equal Holoblastic Cleavage** –

In microlethical and isolecithal egg (with evenly distributed yolk) the entire egg divides producing cells of roughly the same size (or of equal or approx. equal size). Both the first and second mitotic divisions are merifional and at right angles to each other. The plane of the third division is horizontal and at the equator. Aa a result, eight equal blastomeres are formed which divide further to produced approx. equal-sized blastomeres. For example: Amphioxus, marsupial and Placental mammals.

**ii. Unequal Holoblastic Cleavage**-In mesolecthial and telocithal eggs, holoblastic cleavage produces unequal sized blastomeres, which include many small-sized blastomeres called Micromeres and a few large-sized yolk-laden blastomeres called Macromeres. For example, in the eggs of bony fish and amphibians, a moderate amount of yolk is concentrated towards the vegetal pole. It retards the cleavage furrows in the vegetal pole. Both the first and second cleavage is horizontal but above the equator. As a result, the blastomeres produced are unequal. The third cleavage, thus gives rise to four small and four large blastomeres. The large-sized blastomeres contain more yolk, while small-sized blastomeres contain less or no yolk. The large blastomeres are called macromeres or megameres and the smaller ones are called micromeres.

**Cleavage based on symmetry**

Dependent on the cleavage furrow formation and symmetry the holoblastic cleavage is further classified as bilateral, radial, spiral and rotational types.

**a. Bilateral cleavage**

The bilateral cleavages is the result of unequal holoblastic type of division of egg. First bilateral holoblastic cleavage bisects zygote longitudinally into left and right halves. The blastomeres of successive divisions are arranged along a single plane, occurring during first meridional cleavage, divisible into two halve which are mirror images of one anther i.e. the blastomeres are arranged in bilaterally symmetrical manner e.g. vertebrates, some mollusk and some echinoderms.

**b. Radial cleavage**

The radial cleavage occure in equal holoblastic of an egg. In radial cleavage the cell division are equal and symmetrical and occure at right to the polar axis of the egg. The blastula is divisible into two mirror images along axis drawn on any radius i.e. the radially symmetrical. It is characteristic feature of deuterostomes e.g. enchinoderms and Amphioxus.

**c. Spiral cleavage**

In spiral type of cleavage the resultant cells are placed altermate to each other or in a spiral fashion. This type of cleavages usually occurs in equal holoblastic type of cleavages, although some undergo unequal holoblastic cleavages. In this division first two meridional cleavages at right angle to each other giving rise to four daughter cells as A, B, C, and D, each representing one quadrant of an embryo. These two cleavages are parallel to the animal-vegetal axis of the zygote. But at 4-celled stage A and C macromeres meet at animal pole creating animal cross furrow whilst the B and D macromeres meet at vegetal pole creating vegetal cross furrow. It is found in flatworms, annelids and mollusk known as protostomes. In successive cleavage each division occurs at an oblique angle (not right angle to the animal-vegetal axis) to give rise to smaller micromeres know as quartet of the mother cell.

Figure 1.6 : Types of holoblastic cleavages

**d. Rotational cleavage**

In a rotational cleaves normally the first division in along meridionalf the axis giving rise to two daughter cells. But during second cleavages one of the daughter cell divides meridionally whilst the other equatorially. The rotational cleavage is found in isolecithal type of mammalian egg.

Figure 1.7 : Rotational cleavage.

**1.1.4 Meroblastic cleavage**

Meroblastic cleavage means incomplete divisions due the presence of the large amount of yolk preset in macrolecithal egg (telolecithal and centrolecithal egg). These are of three main type bilateral meroblastic cleavage, discoidal and superficial cleavages. The cleavage occurs only in cytoplasm and not in yolk.

**a. Discoidal cleavage**

Many animals have discoidal eggs which contain very little quantity of cytoplasm as compare to huge deposition of yolk. In these eggs the cleavage is restricted to only in cytoplasmic disc, hence the name. The cytoplasmic disc is separated from the yolk by a space called as subgerminal cavity. The discoidal cleavage occurs in fish, reptiles and bird.

**b. Superficial cleavage**

Superficial cleavage is limited to a thin surface area of cytoplasm that covers the entire egg. The center of the egg is filled with yolk which fails to cleave. Thus, the cleavage does not take place in cytoplasm but only nucleus is divided through mitosis, known as karyokinesis. These nuclei are referred as energids. After several rounds of karyokinesis the naked nuclei migrate to the periphery of the egg. At this stage it is called the syncytial blastoderm because all the nuclei share the same cytoplasm. Cellularzation occurs at about the 14$^{th}$ nuclear division to creat the cellular blastoderm. After this time cell divide asynchronously e.g. centrolecithal eggs such as insects.

Figure 1.8: Types of meroblastic cleavages: a. superficial b. discoidal;

**1.2 Types of Blastulae**

The cleavage advances to the multicellular embryonic stage called blastula. The cells of blastula are known as blastomeres. At a later the blastula develops a central cavity known as blastocoel or segmentation cavity, surrounded by multicellular layer called as blastoderm. Mainly three kinds of blastulae are developed in animals e.g. coeloblastula, discoblastula and blastocyst.

Figure 1.9: Coeloblastula and its secondary forms found in lower animals

**Coeloblastula**

Coeloblastula is common in eggs having low yolk content. These are spherical and have centric or eccentric blastocoel. The blastocoel may be made of unilayered or multilayered blastomeres. These are found in Amphioxus, frogs etc. In some lower invertebrates the coeloblastula itself plays a role of larva with little modification e.g. in sponges the stereoblastula, parenchymula and amphiblastula wich directly develop into an adult.

**Discoblastula**

Due to the heavy yolk content the cleavage is arrested at vegetal pole and only occurs at animal pole thus giving rise to polar blastromeres. These form a flat multilayered disc made of blastomeres called blastodisc. Blastodisc hold a space just above the yolk mass called subgerminal cavity or primary blastocoel. The blastodisc remains as a superficial layer detached at the center. The center of the blastodisc therefore remains transparent known as area pellucida as compared to the periphery called as area opaca. The extreme margin of the blastodisc remains attached to the lower yolk mass known as zone of junction. The blastula formed in this manner is known as discoblastula. It is found in reptiles, birds and monotremes whose eggs are of macrolecithal type.

Figure 1. 10: Discoblastula of birds

**Blastocyst**

In marsupial and placental mammals the eggs have almost no yolk. The first cleavage divides egg into two blastomeres out of which one represents animal pole and the other as vegetal pole. Due to the lack of yolk, the cleavage at vegetal pole are faster as compared to that animal pole. The cells at the vegetal pole start growing and dividing vigorously which constitutes the thin outer wall called as trophoblasts (trop=nourish). Finally at the 32 to 64 celled stages the trophoblasts develop an envelope, enclosing an eccentric space, where the yolk would have been, to develop an eccentric slit like cavity, a blastocoel. The cells at animal pole are confined to one end (embryonic pole) often referred to as inner cell mass. The inner cell mass is covered by a layer of Rauber's cells. The blastula thus developed in from zona pellucida and gets implanted on uterine wall. Trophoblasts now start obtaining nourishment from maternal tissue.

Figure 1.11: Blastocyst of mammals.

**1.2 Gastrulation**

Gastrulation is a phenomenon of making and shaping the embryo by the course of massive proliferation, movements and rearrangement of the cells occurred in a simple multicellular ball, the blastula. The cell movements locate them to their definitive position in the embryo which leads to the formation of basic germ layers (embryonic layers) which play important role in organogenesis. These germ layers are formed due to various cellular activities such as cell motility, their shaping and adhesion known as morphogenetic movements. During these movements, a new cavity is developed called archenteron (gastrocoel) which opens to exterior by a blastopore. Invertebrates like poriferans and coelenterates exhibit very simple gastrulation developing only two germ layers viz. ectoderm and endoderm. These are referred as diploblastic animals.

Figure 1.12: Scheme of germ layers in diploblastic and triploblastic animals

Formation of planula larva in coelenterates is classical example of diploblastic gastrula developing into an adult. In higher animals, three germ layers viz. outermost ectoderm, middle mesoderm and innermost endoderm, are formed hence they are known as triploblastic. Endoderm forms inner lining of the gut and many internal organs like kidney, urinary bladder etc. Ectoderm forms external structures like skin, nervous system, exoskeleton etc. Mesoderm develops into muscles, skeletal and circulatory systems. Archenteron develops into muscles, skeletal and circulatory systems. Archenteron develops into gut of the animal. In lower invertebrates in which the blastopore develops into mouth are referred to as protostomes (phylum: Porifera to Phylum: Mollusca) while in higher animals it forms anus and mouth develops opposite to it are called as deuterostomes (Phylum: Echinodermata and above).

**1.1.4 Morphogenetics Movements:**

Morphogenetics movements are of two major types viz. epiboly and emboly .Epiboly is a process of thinning and extension of the epithelium which occurs through different movements of the embryonic cells as a whole e.g. extension ,intercalation convergence, divergence, etc. whereas, emboly involves the movements of cells into the interior of embryo e.g. invagination ,ingression, infiltration ,delamination ,proliferation and involution.

**Types of movements in epiboly:**

Extension: Here the cells get stretched to increase the length of the germ layer.

Intercalations: It is merging of two epithelia in which cells from two adjacent epithelia move between one another and merge to form a single layer.

Convergence /divergence: It means the intercalation of cells from multilayered epithelium in a highly directional and organized manner .When cells congregate at one point the process is called convergence and incase they move away from each other is known as divergence .

Mostly all these movements occur in combinations.

**Types of movements in emboly**

Invagination: The layers of epithelial cells migrates inwards and forms a depression. The region from where the cells invaginate s called the blastopore. It has a dorsal lip and a ventral lip. The dorsal lip is made of apical cells and the ventral of the basal cells. This is seen in Amphioxus, frog.

Figure 1.14: Types of cell movements in gastrulation

**Ingression:** The epithelial cells get separated and migrate inside to form free flowing mesenchymal cells to get rearranged in the gastrulation process. It is seen in echinoderms.

**Involution:** The epithelial layer rolls down and folds inwards to form a new layer underneath the outer layer. It is seen in amphibians and birds.

**Infiltration:** The cells detach and fall inside the lumen of the embryo (blastocoel)

To form loose cell mass called as mesenchyme. The mesenchyme cells then spread out quickly to form a continuous layer called hypoblast. The blastocoel is now called as archenteron. It is seen in chick and human.

Epiboly showing extension, intercalation, convergence and extension

**Delamination:** The cells get divided equatorially to form a new layer which ultimately gets separated by splitting up from the mother layer. It is seen in mammals

Figure 1.15: The process of emboly involved in gastrulation of animal embryos

**Gastrulation in protochordates having microlecithal egg (example: Amphiouxs)**

The gastrulation in amphioxus occurs by the process of invagination forming initially a double layered cup. The blastocoel reduces by the course of development of the gastrula and the cup shaped formation holds a new cavity known as archenteron. As the gastrulation advances the opening of the cup constricts to form blastopore. At this stage the gastrula exhibits outer ectoderm and the inner endoderm with rudiments of mesoderm.

Figure: 1.16: Gastrulation in Amphioxus

**Gastrulation in amphibian with mesolecithal egg of frog**

Due to the presence of adequate yolk the process of invagination of the blastula is restricted only towards animal pole. Initially an inverted crescentic depression (slit-like) occurs at the equator. The upper margin of this slit is named as dorsal lip of blastopore. The micromeres at animal pole divide rapidly and migrate towards the vegetal pole to cover the macromeres through epiboly. During this process the macromeres shift inside by process of involution and invagination (emboly). The entire mass of macromeres move inside except a small portion which is visible from the blastopore called as yolk plug. The embryo becomes double walled gastrula enclosing archenteron opening to exterior with a blastopore. The macromeres constitute the endoderm lining internal layer of the gastrula and the outer micromere layer becomes ectoderm. Some cells at the blastopore undergo ingression to from third germ layer called mesoderm.

Figure: 1.17: Gastrulation in frog

**Gastrulation in bird with macrolecithal egg.**

In discoblastula of birds, the blastoderm remains as superficial layer, the epiblast. The lower layer, the hypoblast is formed through the phenomenon of several processes (as explained by number of theorise) of epiblast cells underneath. The hypoblast divides the divides the subgerminal cavity into dorsal true blastocoel and ventral, the archenteron. It has been stated that the cells forming endoderm migrate from posterior to anterior direction of the embryo. The formation of mesoderm initiates with the origin of primitive streak developed at posterior end along the mid-dorsal line of the discoblastula. The primitive streak later grows forward and elongates. The thickening of the primitive streak occurs due to convergence of epiblast cells due to the presence of underlying hypoblast cells. There is a furrow lying mid-dorsally to the primitive streak called primitive groove which forms primitive folds at the lateral edges. At anterior end of the primitive groove is a compact mass of the cells called Hensen’s node at the lateral edges. At anterior end of the primitive pit. At posterior end, the primitive steak has a plate called primitive plate. As the primitive streak elongates towards the anterior end, the area pellucida gets thickened and forms elliptical embryonic shield. The mesenchyme cells proliferate rapidly near the primitive groove and migrate to occupy blastocoel present between epiblast and hypoblast. They continue migrating antero-laterally unto the limit of primitive streak. These mesenchyme cells proliferate rapidly near the primitive groove and migrate to occupy blastocoel present between epiblast and hypoblast. They continue migrating antero-laterally unto the limit of primitive streak. These mesenchyme cells constitute the mesoderm. With the advancement of the embryo, the primitive streak disintegrates and recedes backwards dragging Hensen’s node along. The Hensen’s node goes on releasing behind the prechordal and notochordal cells (modified epiblast cells) which ultimately develop into nerve cord and notochord respectively. The primitive streak disintegrates in such a manner that its remnants restrict merely to the tail and cloacal region of the hatchling. Nevertheless, the epiblast and hypoblast later become ectoderm and endoderm, respectively. The mesoderm free area lying anterior to primitive streak is called as proamnion. The proamnion region plays a role in the formation of a distinct head known as ceahalization.

Figure 1.18: Gastrulation in birds

**Gastrulation in mammal with alecithal egg**

It has been believed that the trophoblasts after hatching out of zona pellucida absorb the surrounding uterine fluid for their nourishment to grow and multiply faster. Trophoblasts play important role in formation of a placenta. In mammals, the gastrulation initiates with the horizontal division of inner cell mass of blastocyst by the process of delamination to give rise to upper epiblast and the lower hypoblast. The hypoblast grows downwards to across the inner lining of trophoblasts to form endoderm. Endoderm, Eventually meets mid-ventrally to enclose blastocoel to form archenteron or yolk sac. The Rauber's cells now disintegrate to expose epiblast which develops into polar disc or embryonic disc by multiplication and rearrangement of the remaining inner cell mass. The upper cell-layer of this embryonic disc then merges with trophoblasts to form ectoderm which is then called trophectoderm. Trophectoderm also in due course of time extends over the whole embryo to form outer germ layer.

Development of primitive streak and subsequent formation of mesoderm initiate after the formation of trophectoderm. Formation of primitive streak involves rapid multiplication of the cell in the causing thickening of the area. Initially, an elongated primitive streak originates at the caudal end in the form of a crescentic outgrowth and extends towards the cephalic end of the embryo. Due to the crowing of cells along the sides of the primitive streak, there occurs ingression of some cells to form mesenchyme cell layer between the endoderm and trophectoderm. The mesenchyme cells later start multiplying and migrating antero-laterally to occupy the space between ectoderm and endoderm to modify into a middle germ layer, the embryonic mesoderm. The ingression of mesenchyme cells also occurs outside the embryonic disc to form extraembryonic mesoderm. The extra-embryonic mesoderm plays an important role in the development of extraembryonic (foetal) membranes.