B. Sc. Semester VI (Paper: CC-13)
Developmental Biology
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Gastrulation

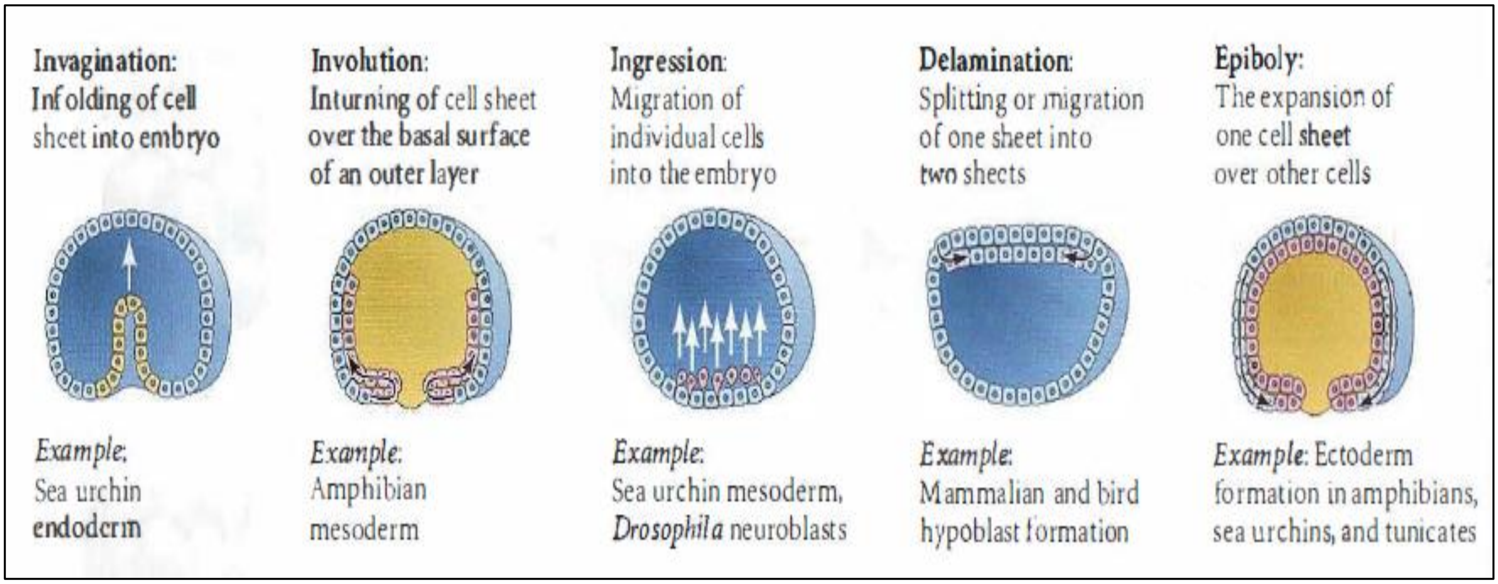
According to Balinsky (1981), gastrulation is a dynamic process in which one cell layered blastula by morphogenetic movements of cells, is converted into a three layered (ectoderm, endoderm and mesoderm) grastula, is known as gastrulation.

The blastula consists of numerous cells, the positions of which were established during cleavage. During gastrulation, these cells are given new positions and new neighbors, and the multilayered body plan of the organism is established. 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. Thus, the three germ layers-outer ectoderm, inner endoderm, and interstitial mesoderm-are first produced during gastrulation. In addition, the stage is set for the interactions of these newly positioned tissues.

Gastrulation usually involves some combination of several types of movements. These movements involve the entire embryo, and cell migrations in one part of the gastrulating embryo must be intimately coordinated with other movements that are taking place simultaneously.

Although patterns of gastrulation vary enormously throughout the animal kingdom, there are only a few basic types of cell movements:

- **Invagination:** The infolding of a region of cells, much like the indenting of a soft rubber ball when it is poked.
- **Involution:** The inturning or inward movement of an expanding outer layer so that it spreads over the internal surface of the remaining external cells.
- **Ingression:** The migration of individual cells from thesurface layer into the interior of the embryo. The cel1s become mesenchymal (i,e., they separate from one another) and migrate independently.
- **Delamination:** The splitting of one cellular sheet into two more or less parallel sheets. While on a cellular basis it resembles ingression, the result is the formation of a new sheet of cells.
- **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 embtyo, Epiboly can occur by the cells dividing, by the cells changing their shape, or by several layers of cells intercalating into fewer layers. Often, all three mechanisms are used.



Types of cell movements during gastrulation.

Significance of gastrulation

1. Due to morphogenetic movements various arrangements of the cells take place.
2. Rate of cell division gradually diminishes
3. Rate of oxidation increases
4. Qualitative increase of metabolism takes place
5. Nucleus becomes more active in the activities of embryonic cells.
6. Presumptive structures are placed in the right position of the embryo
7. For the morphogenesis of the nervous system gastrulation is very important.

Gastrulation of Frog

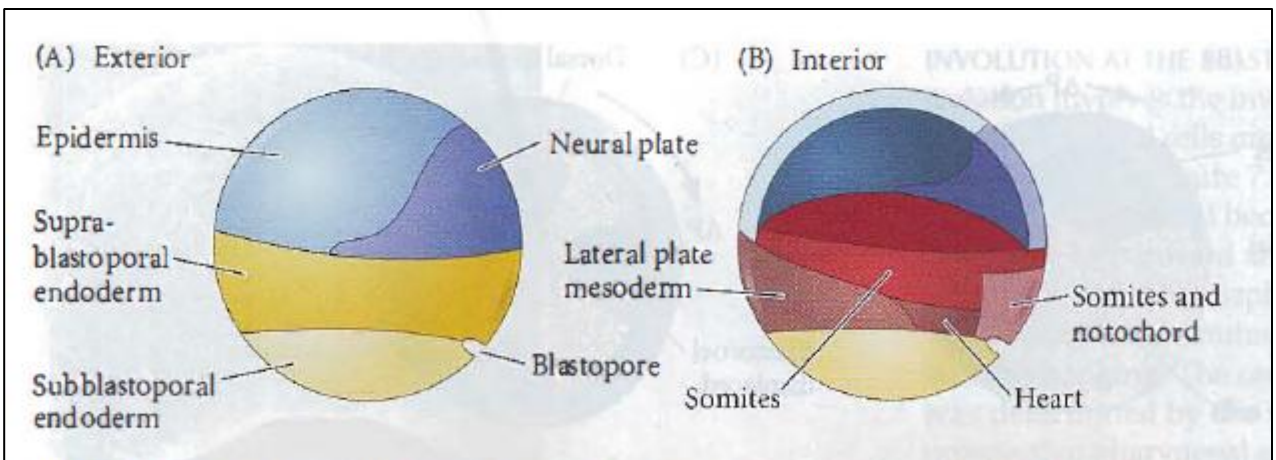


FIGURE 7.5 Fate maps of the *Xenopus laevis* blastula exterior (A) and interior (B). Most of the mesodermal derivatives are formed from the interior cells. The placement of ventral mesoderm remains controversial (see Kumano and Smith 2002; Lane and Sheets 2006). (After Lane and Smith 1999; Newman and Kreig 1999.)

Each embryonic germ layer contributes to a distinct set of structures in the adult animal. The embryonic organization of the germ layers is often reflected in the adult: The ectoderm forms the nervous system and outer body layer, the mesoderm gives rise to muscles and skeleton, and the endoderm lines many organs and ducts. There are, however, numerous exceptions.

Figure 47.9 Major derivatives of the three embryonic germ layers in vertebrates.

ECTODERM (outer layer)	MESODERM (middle layer)	ENDODERM (inner layer)
• Epidermis of skin and its derivatives (including sweat glands, hair follicles) • Nervous and sensory systems • Pituitary gland, adrenal medulla • Jaws and teeth	• Skeletal and muscular systems • Circulatory and lymphatic systems • Excretory and reproductive systems (except germ cells) • Dermis of skin • Adrenal cortex	• Epithelial lining of digestive tract and associated organs • Epithelial lining of respiratory, excretory, and reproductive tracts and ducts • Thymus, thyroid, and parathyroid glands

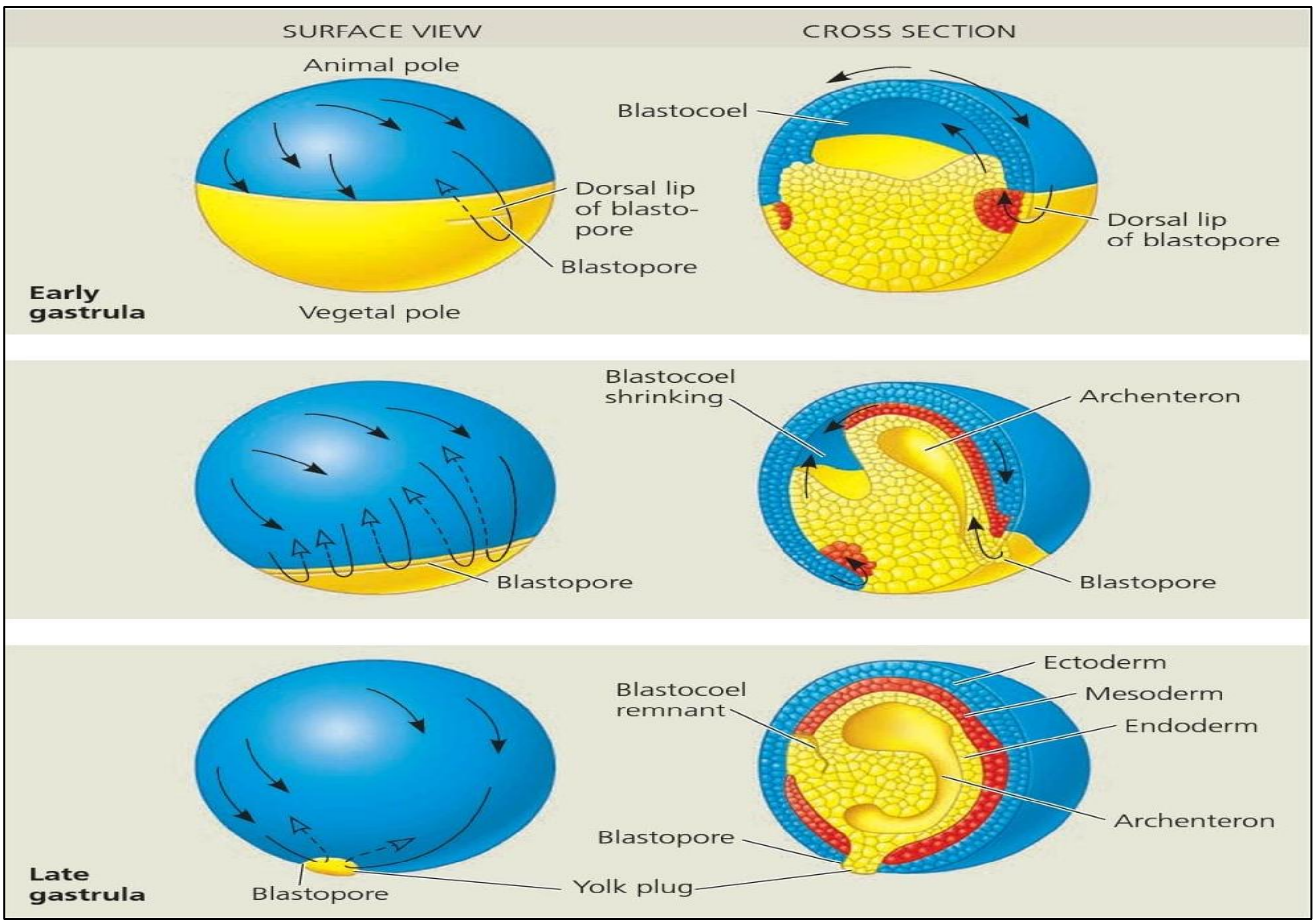


Figure: Gastrulation in a frog embryo. In the frog blastula, the blastocoel is displaced toward the animal pole and is surrounded by a wall several cells thick.

Four type of morphogenetic movements takes place in gastrulation process of frog-

1. Vegetal rotation and the invagina tion of thebottle cells
2. Involution at the blastopore lip
3. Convergent extension of the dorsal mesoderm
4. Epiboly o f the prospective ectoderm

Gastrulation begins when cells on the dorsal side invaginate to form a small indented crease, the blastopore. The part above the crease is called the dorsal lip. As the blastopore is forming, a sheet of cells begins to spread out of the animal hemisphere, rolls inward over the dorsal lip (involution), and moves into the interior (shown by the dashed arrow). In the interior, these cells will form endoderm and mesoderm, with the endodermal layer on the inside. Meanwhile, cells at the animal pole change shape and begin spreading over the outer surface.

The blastopore extends around both sides of the embryo as more cells invaginate. When the ends meet, the blastopore forms a circle that becomes smaller as ectoderm spreads downward over the surface. Internally, continued involution expands the endoderm and mesoderm; an archenteron forms and grows as the blastocoel shrinks and eventually disappears.

Late in gastrulation, the cells remaining on the surface make up the ectoderm. The endoderm is the innermost layer, and the mesoderm lies between the ectoderm and endoderm. The circular blastopore surrounds a plug of yolk-filled cells.

TABLE 7.1 Results of tissue transplantation during early- and late-gastrula stages in the newt

Donor region	Host region	Differentiation of donor tissue	Conclusion
EARLY GASTRULA			
Prospective neurons	Prospective epidermis	Epidermis	Conditional development
Prospective epidermis	Prospective neurons	Neurons	Conditional development
LATE GASTRULA			
Prospective neurons	Prospective epidermis	Neurons	Autonomous development (determined)
Prospective epidermis	Prospective neurons	Epidermis	Autonomous development (determined)

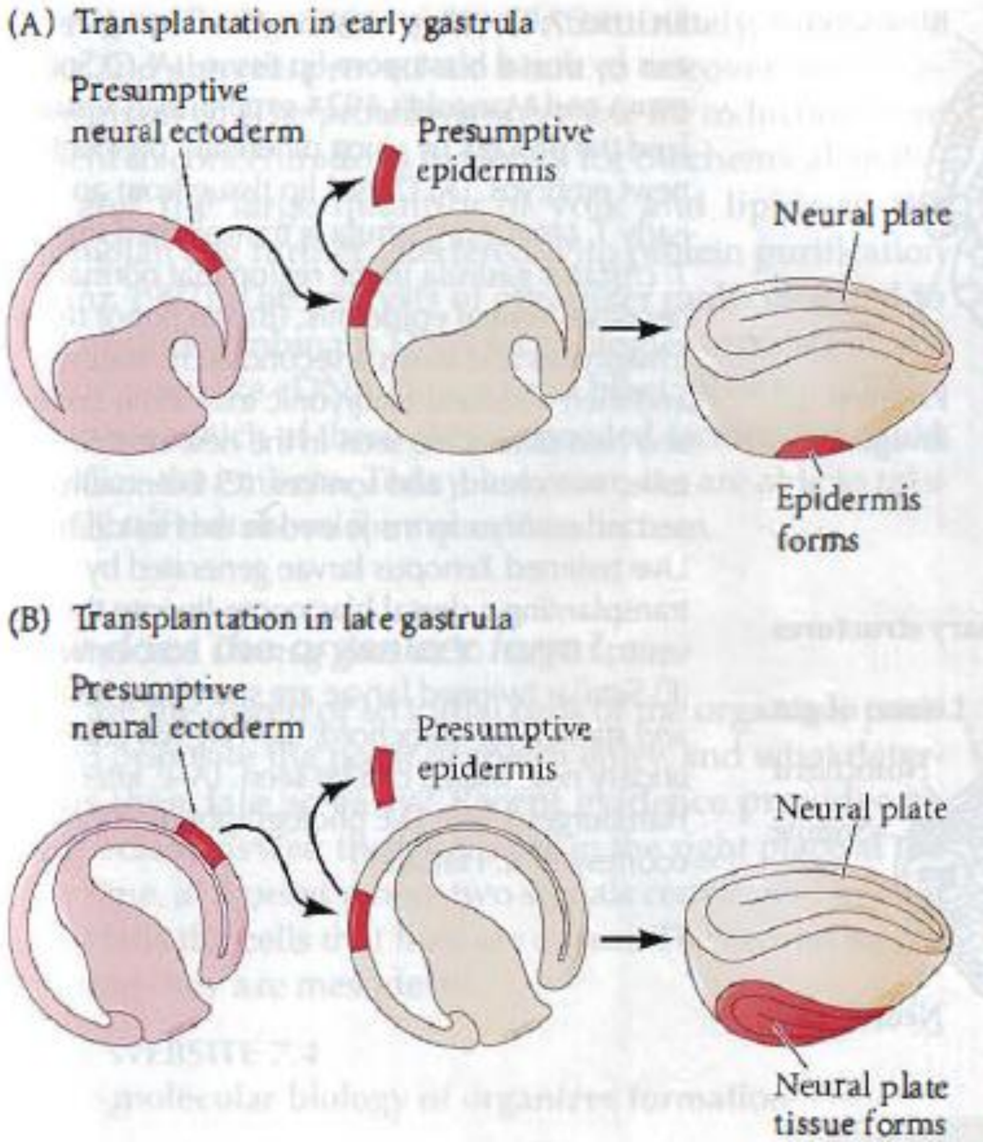
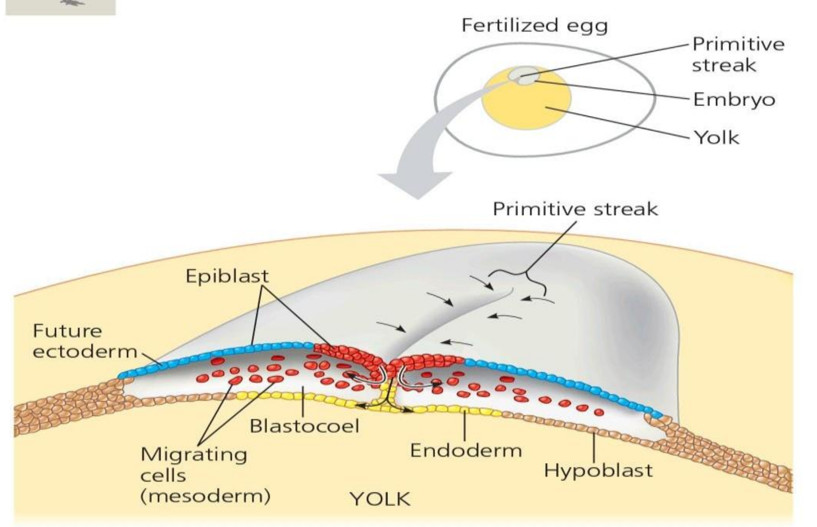


FIGURE 7.16 Determination of ectoderm during newt gastrulation. Presumptive neural ectoderm from one newt embryo is transplanted into a region in another embryo that normally becomes epidermis. (A) When the tissues are transferred between early gastrulae, the presumptive neural tissue develops into epidermis, and only one neural plate is seen. (B) When the same experiment is performed using late-gastrula tissues, the presumptive neural cells form neural tissue, thereby causing two neural plates to form on the host. (After Saxén and Toivonen 1962.)

Gastrulation in Chicks

Gastrulation in Chicks At the onset of gastrulation in chicks, an upper and a lower layer of cells—the epiblast and hypoblast—lie atop a yolk mass. All the cells that will form the embryo come from the epiblast. During gastrulation, some epiblast cells move toward the midline, detach, and move inward toward the yolk. The pileup of cells moving inward at the midline produces a visible thickening called the primitive streak. Some of these cells move downward and form endoderm, pushing aside the hypoblast cells, while others migrate laterally (sideways) and form mesoderm. The cells left behind on the surface at the end of gastrulation will become ectoderm. The hypoblast cells later segregate from the endoderm and eventually form part of the sac that surrounds the yolk and also part of the stalk that connects the yolk mass to the embryo. Although different terms describe gastrulation in different vertebrate species, the rearrangements and movements of cells exhibit a number of fundamental similarities. In particular, the primitive streak for the chick embryo, is the counterpart of the blastopore lip for the frog embryo.

Figure 47.11 Gastrulation in a chick embryo. This is a cross section of a gastrulating embryo, looking toward the anterior end.



The hypoblast

By the time a hen has laid an egg, the blastoderm contains some 20,000 cells. At this time, most of the cells of the area pellucida remain at the surface, forming an "upper layer," called the epiblast, while other area pellucida cells have delaminated and migrated individually into the subgerminal cavity to form hypoblast islands (sometimes called the primary hypoblast or polyinvaginatiolt islands), an archipelago of disconnected clusters of 5-20 cells each. Shortly thereafter, a sheet of cells derived from deep yolky cells at the posterior margin of the blastoderm migrates anteriorly beneath the surface. This sheet of migrating cells pushes the hypoblast islands anteriorly, thereby forming the secondary hypoblast, or endoblast. The resulting two-layered blastoderm (epiblast and hypoblast) is joined together at the mar. ginal zone of the area opaca, and the space between the layers forms a blastocoel.

Formation of the Primitive Streak

The streak is first visible as cells accumulate in the middle layer, followed by a thickening of the epiblast at the posterior marginal zone, just anterior to Koller's sickle. This thickening is initiated by an increase in tile height (thickness) of the cells fOrming the center of the primitive streak.

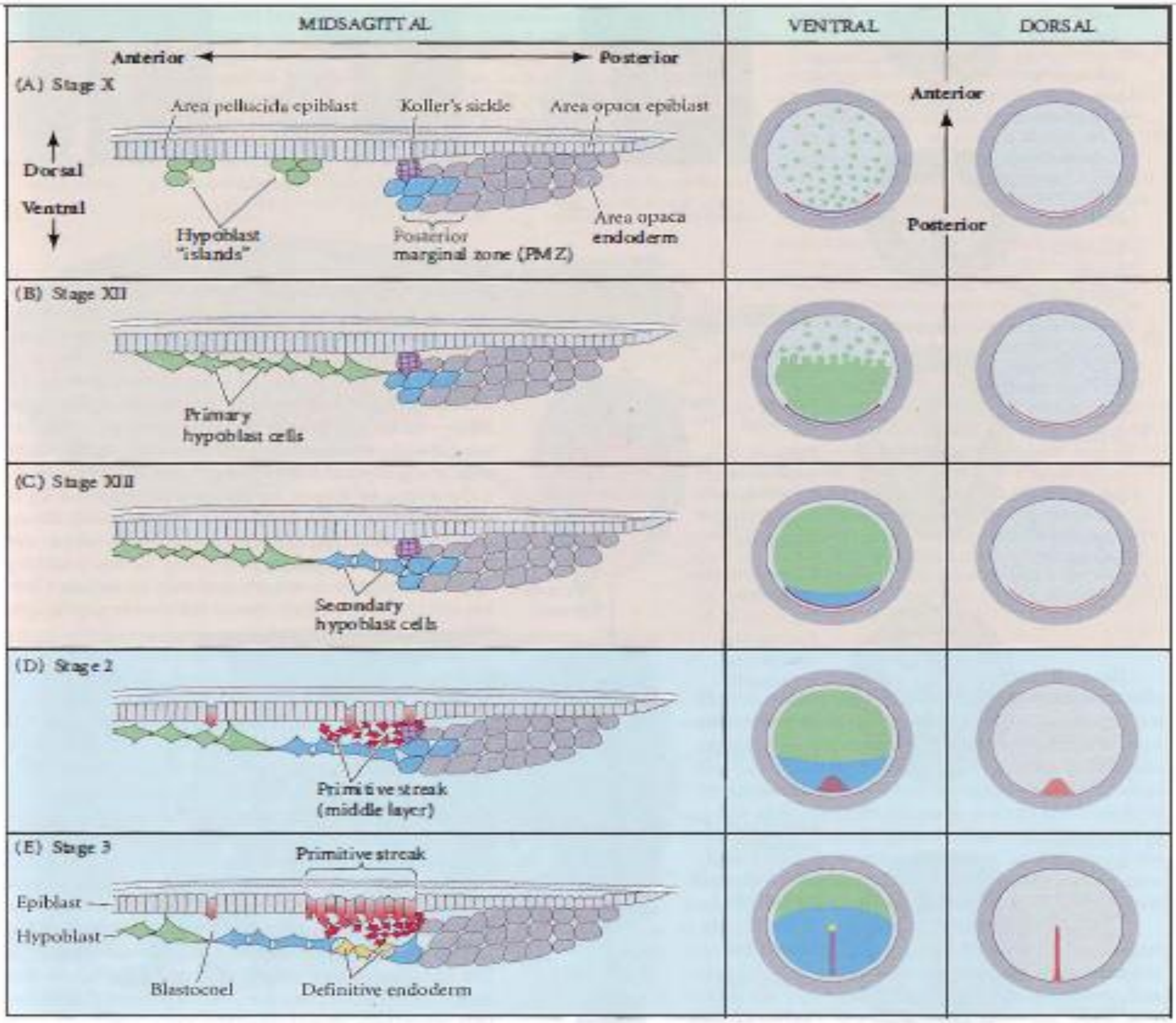


FIGURE 8.2 Formation of the chick blastoderm. The left column depicts a diagrammatic midsagittal section through part of the blastoderm. The middle column depicts the entire embryo viewed from the ventral side. This shows the migration of the primary hypoblast and the secondary hypoblast (endoblast) cells. The right column shows the entire embryo seen from the dorsal side. (A–C) Events prior to laying of the shelled egg. (A) Stage X embryo, where islands of hypoblast cells can be seen, as well as a congregation of hypoblast cells around Koller's sickle. (B) By stage XII, just prior to primitive streak formation, the hypoblast island cells have coalesced to form the primary hypoblast layer, which meets endoblast cells and primitive streak cells at Koller's sickle. (C) By stage XIII, the secondary hypoblast cells migrate anteriorly. (D) By stage 2 (6–7 hours after the egg is laid), the primitive streak cells form a third layer that lies between the hypoblast and epiblast cells. (E) By stage 3 (up to 13 hours post laying), the primitive streak has become a definitive region of the epiblast, with cells migrating through it to become the mesoderm and endoderm. (After Stern 2004.)

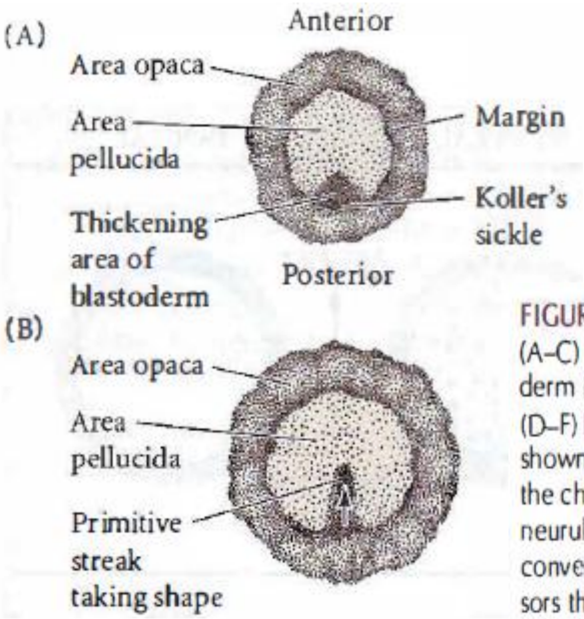
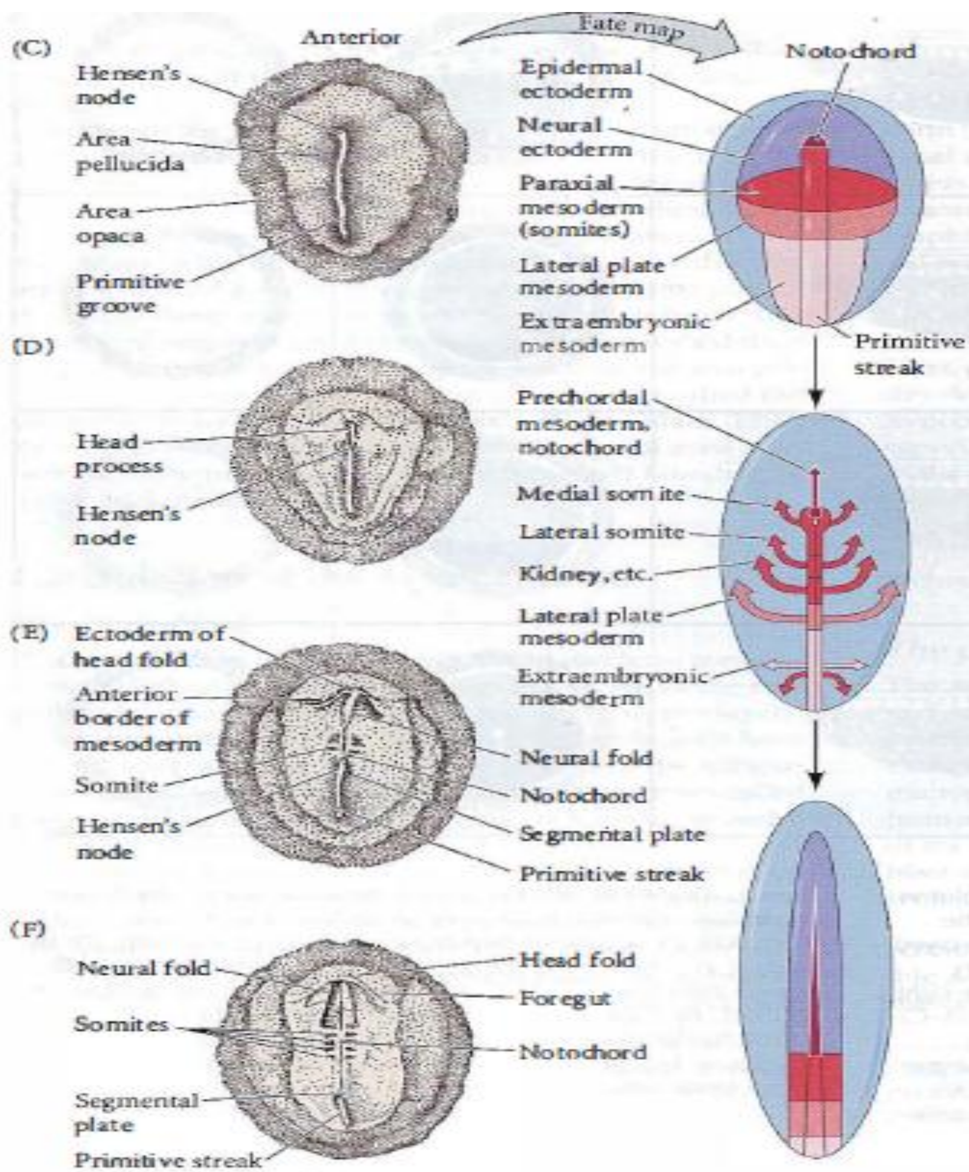


FIGURE 8.3 Cell movements of the primitive streak and fate map of the chick embryo. (A–C) Dorsal view of the formation and elongation of the primitive streak. The blastoderm is seen at (A) 3–4 hours, (B) 7–8 hours, and (C) 15–16 hours after fertilization. (D–F) Formation of notochord and mesodermal somites as the primitive streak regresses, shown at (D) 19–22 hours, (E) 23–24 hours, and (F) the four-somite stage. Fate maps of the chick epiblast are shown for two stages, the definitive primitive streak stage (C) and neurulation (F). In (F), the endoderm has already ingressed beneath the epiblast, and convergent extension is seen in the midline. The movements of the mesodermal precursors through the primitive streak at (C) are shown. (Adapted from several sources, especially Spratt 1946; Smith and Schoenwolf 1998; Stern 2005a,b.)



Elongation of the Primitive Streak

As cells enter the primitive streak, they undergo an epithelial-to-mesenchymal transformation, and the basal lamina beneath them breaks down. The streak elongates toward the future head region as more anterior cells migrate toward the center of the embryo.

Formation of Endoderm and Mesoderm

As soon as the primitive streak has formed, epiblast cells begin to migrate through it and into the blastocoel. The streak thus has a continually changing cell population. Cells migrating through the anterior end pass down into the blastocoel and migrate anteriorly, forming the endoderm, head mesoderm, and notochord; ceUs passing through the more posterlor portions of the primitive streak give rise to the majority of mesodermal tissues.

Migration through the Primitive Streak

The migration of the mesodermal cells through the anterior primitive streak and their condensation to form the chordamesoderm appear to be controlled by FGF signaling. Fgf8 protein is expressed in the primitive streak and repels migrating cells away from the streak.

Meanwhile, cells continue migrating inward through the primitive streak. As they enter the embryo, the cells separate into two layers. The deep layer joins the hypoblast along its midline, displacing the hypoblast cells to the sides. These deep-moving cells give rise to all the endodemlal organs of the embryo, as well as to most of the extraembryonic membranes (the hypoblast and peripheral cells of the area opaca form the rest). The second migrating layer spreads to form a loose layer of cells between this endoderm and the epiblast. This middle layer of cells generates the mesodermal portions of the embryo and the mesoderm lining the extraembryonic membranes.

Movement away from the streak appears to be guided by Fgf8-mediated chemo-repulsion, and the further movement of the mesodermal precursors appears to be regulated by Wnt proteins. In the more posterior regions, Wnt5a is unopposed and directs the cells to migrate broadly to become the lateral plate mesoderm. In the more anterior regions of the streak, however, Wnt5a is opposed by Wnt3a, which inhibits migration and causes the cells to form paraxial mesoderm. Indeed, the addition of Wnt3asecreting pellets to the posterior primitive streak suppresses lateral migration and prevents the formation of lateral plate mesoderm.

Regression of the primitive streak and epiboly of the ectoderm

Now a new phase of development begins. As mesodermal ingression continues, the primitive streak starts to regress, moving Hensen's node from near the center of the area pellucida to a more posterior position. The regressing streak leaves in its wake the dorsal axis of the embryo, including the notochord. The notochord is laid down in a head-to-tail direction, starting at the level where the ears and hindbrain form and extending caudally to the tail bud. While the presumptive mesodermal and endodermal cells are moving inward, the ectodermal precursors proliferate and migrate to surround the yolk by epiboly.

Thus, as avian gastrulation draws to a dose, the ectoderm has surrounded the yolk, the endoderm has replaced the hypoblast, and the mesoderm has positioned itself between these two regions. Although we have identified many of the processes involved in avian gastrulation, we are only beginning to understand the molecular mechanisms by which some of these processes are carried out.