

Biology 340
Comparative Embryology
Lecture 8
Dr. Stuart Sumida

Introduction to Amniota; Vertebrata

Extant Birds (Chicken) as our
analog for basal Amniota

PHYLOGENETIC CONTEXT:

We will now continue our examination of early development in vertebrates. Recall the three different types of eggs based on yolk type, micro-, meso- and macrolecithal eggs.

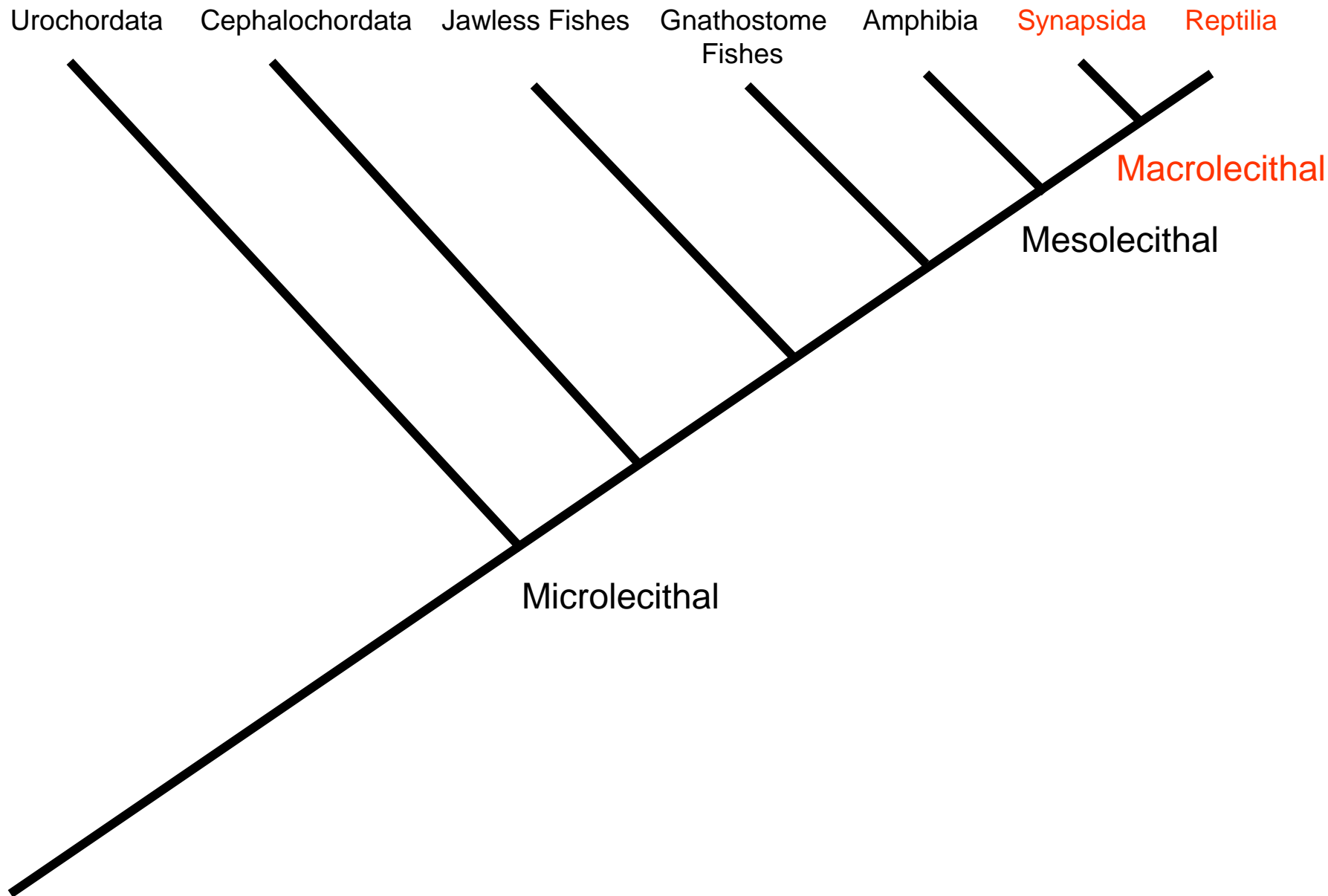
In our rough “morphological series” (a series of extant taxa used to demonstrate our best estimate of actual phylogenetic progression), we now examine:

Microlecithal – Amphioxus

Mesolecithal – Amphibian (frog)

Macrolecithal – Bird (as model of basal reptile)

(Back to) Microlecithal – Therian mammal.



Many of the differences in the early development of amphioxus and the early development of frogs may be ascribed to two major things: (1) the difference in the amount of yolk present; and (2) presence of neural crest.

Here we'll see that the ovum (egg) of the chicken is MACROLECITHAL, containing a large amount of yolk. In this lecture, the chicken egg will be our analog for the condition in basal amniotes such as monotremes, reptiles and birds.

INTRODUCTION TO AMNIOTE DEVELOPMENT: AVES

The ontogeny of birds is sufficiently like that of reptiles to satisfy the position of a basal amniote in our morphological series. And, because of its ready availability, the chicken is better known in its development than any other bird or reptile.

We won't bother with the development of the egg shell. Instead we will press on to actual embryonic development.

To the cook, the entire contents of the shell are the “egg”, but only the part the cook would call the yolk is the actual ovum. This ovum is macrolecithal – it has a great deal of yolk. Further, the yolk is placed eccentrically. That is, it is TELOLECITHAL.

For now we will only follow the development of a small part of the yolk, the portion where the embryo will form. That area is called the **BLASTODISC**.

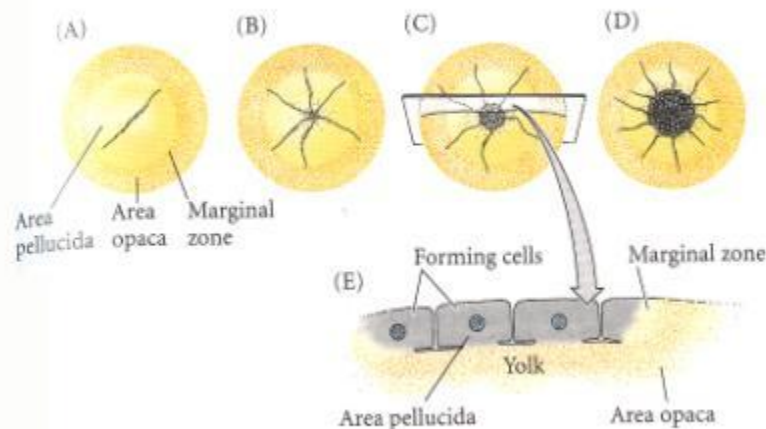


The portion of the blastodisc is actually very small. All of the rest of the egg is “EXTRA-EMBRYONIC”.

EARLY CLEAVAGE

Cleavage is restricted to the blastodisc. It is not holoblastic as cleavage does not pass through the entire egg. For this reason they are termed **MEROBLASTIC**. In fact they fall far short of complete cleavage. At first they don't even pass entirely through the blastodisc. What we see are only furrows.

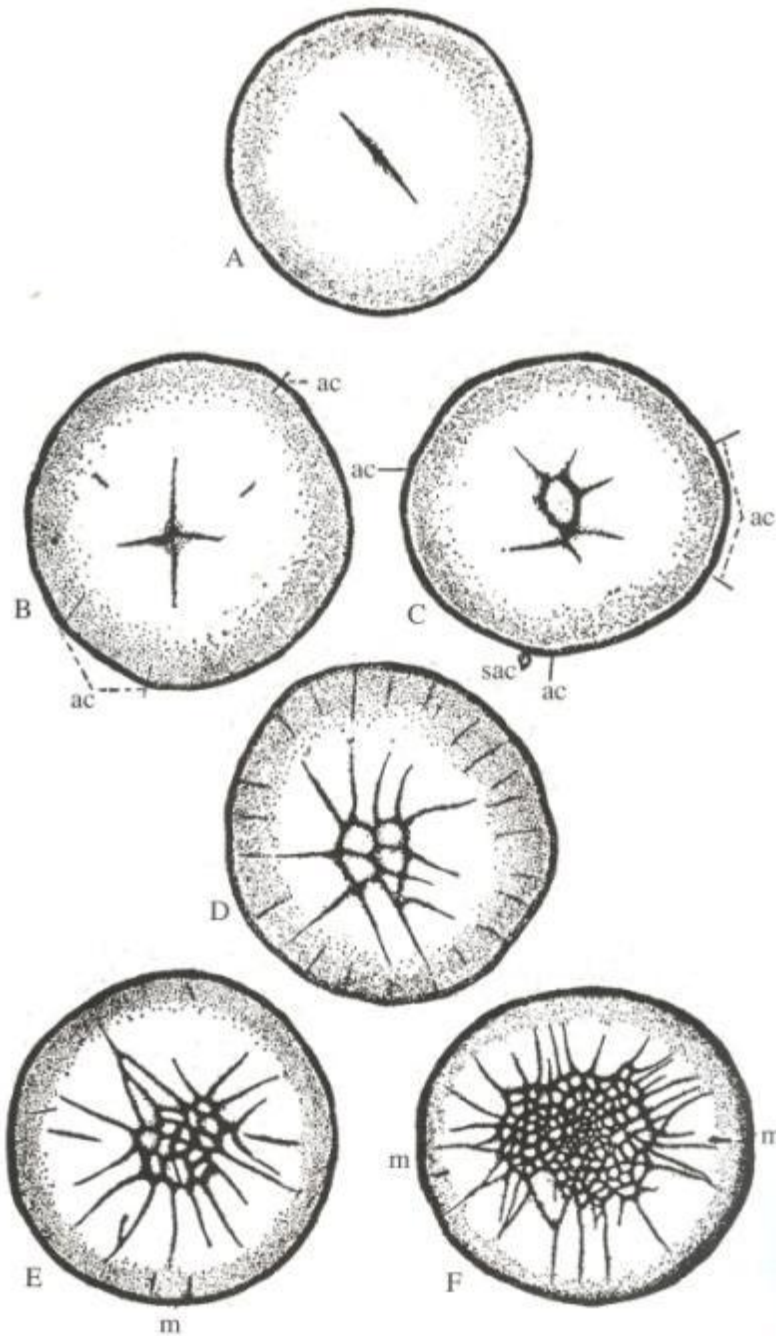
The first two furrows are at right angles to one another. The next set of two furrows lies at right angles to the second cleavage furrow. The furrows do not even reach the edge of the blastodisc.



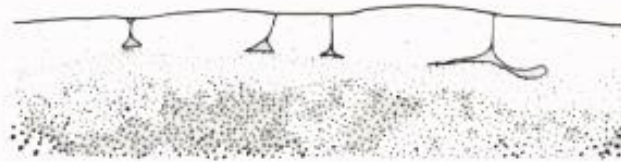
After awhile we can distinguish two groups of blastomeres:

- Central blastomeres that are completely bounded

- Marginal blastomeres that are continuous with the rest of the undivided blastodisc.



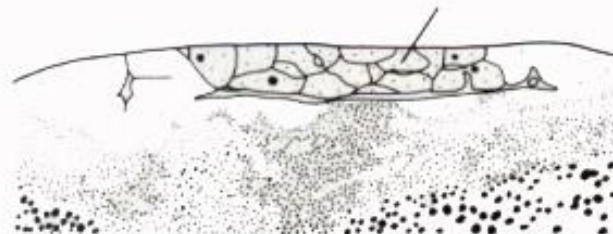
Active cytoplasm



Cavity between blastomeres and yolk



Blastoderm = blastodisk

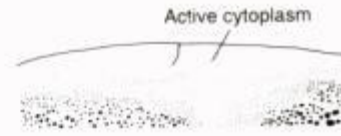




2



1



Active cytoplasm



4



2



Cavity between blastomeres and yolk



8



4



Blastoderm = blastodisk



16



8



Macrolecithal egg
Most fishes, reptiles, birds
Meroblastic cleavage

Blastomeres



Blastocoele

Animal cells



Vegetal cells

Microlecithal egg
Amphioxus
Holoblastic cleavage

Blastocoele



Mesolecithal egg
Amphibians
Holoblastic cleavage

SUBGERMINAL SPACE

Eventually a multilayered plate is formed with a cavity beneath it. This multilayered plate is called the BLASTODERM.

The cavity below it is called the SUBGERMINAL SPACE. The embryo proper will develop in the portion above the subgerminal space, away from direct contact with the yolk.

Illustrate Subgerminal space here:

THE “BLASTULA” STAGE

Limiting our attention to the blastoderm above the subgerminal space, we notice that some of the cells (randomly scattered at first) are somewhat more heavily laden with yolk than others.

Illustrate “blastula” embryo here:

HYPOBLAST FORMATION

As the yolky cells are larger and more heavily laden, they migrate down closer to the subgerminal space. Thus there is a splitting away of the yolky cells from the not-so-yolky cells.

This process is called DELAMINATION. It results in a two-layered embryo. The upper layer is called the EPIBLAST and the lower layer is called the HYPOBLAST. Ultimately, the hypoblast becomes the endoderm.

Illustrate the bilaminar embryo here:

Then, a space develops between the epiblast and the hypoblast.

Illustrate “blastocoele” stage here:

The hypoblast does not form immediately as a full blown layer.

It first appears “posteriorly”. After initial delamination, via multiplication of cells, it also spreads forward and laterally to make the full layer.

Also, there is a very small involution of supplementary endodermal cells. Because some involution takes place, some would call this a ‘gastrula stage’.

Some workers would call the “blastocoele” the equivalent of the archenteron, as it is a space that is at least partially bounded by endodermal cells.

We must note here that there is some debate as to whether this stage would be called a “blastula” or a “gastrula”. If the space between the epiblast and the hypoblast is indeed homologous to the blastocoele, it is at least a blastula. IF one of these spaces was homologous to the archenteron, then it could be called a “gastrula”. Of course, the developing bird could care less.

It is sufficient to say that the endoderm does not go through any lengthy migrations or involutions to reach its current differentiated position. There is very little turning in of endodermal cells.

This is a considerable ACCELERATION as compared to the lengthy and energetically expensive invaginations that we saw in amphioxus and amphibians.

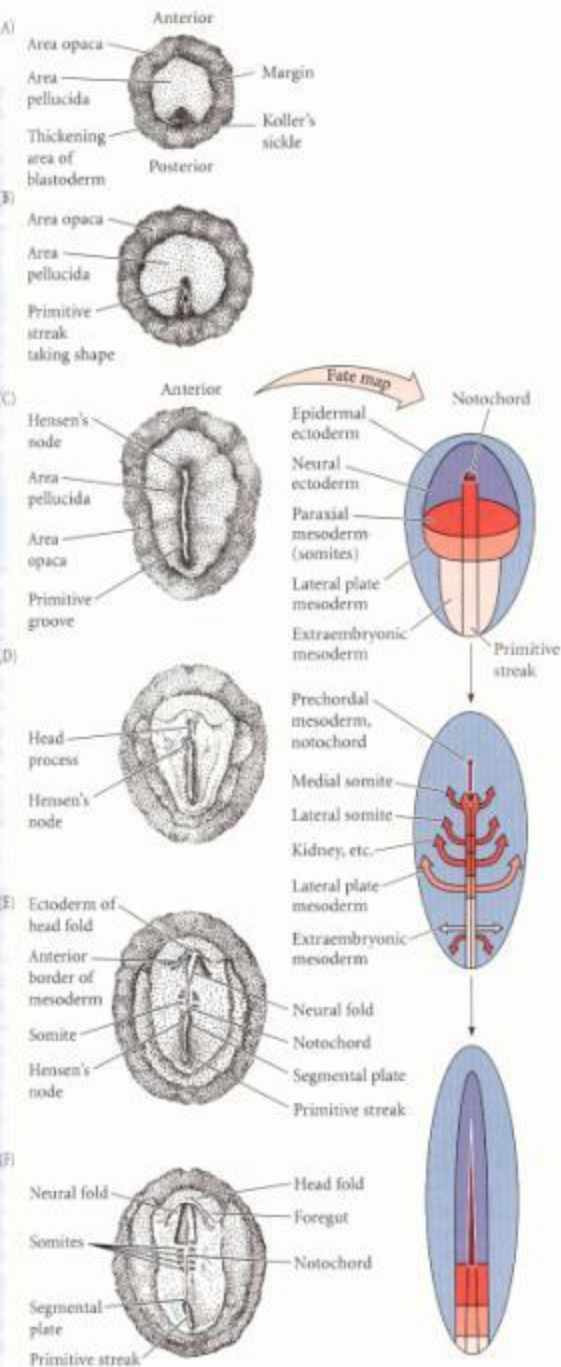
Note that this is a relative acceleration in that the endoderm is differentiated prior to the distinction of the notochordal mesoderm or other mesoderm in birds.

This is an example of the fact that ontogenies evolve. In fact some would suggest that the “gastrocoele” develops before the blastocoele in birds. This is also a change in developmental timing.

A change in developmental timing or order is known as
HETEROCHRONY.

FATE MAP

At this delamination stage, we could plot on to the surface of the epiblast the areas that give rise to: epidermal ectoderm, neural ectoderm, notochord (chordamesoderm), mesoderm (lateral mesoderm), prechordal mesoderm

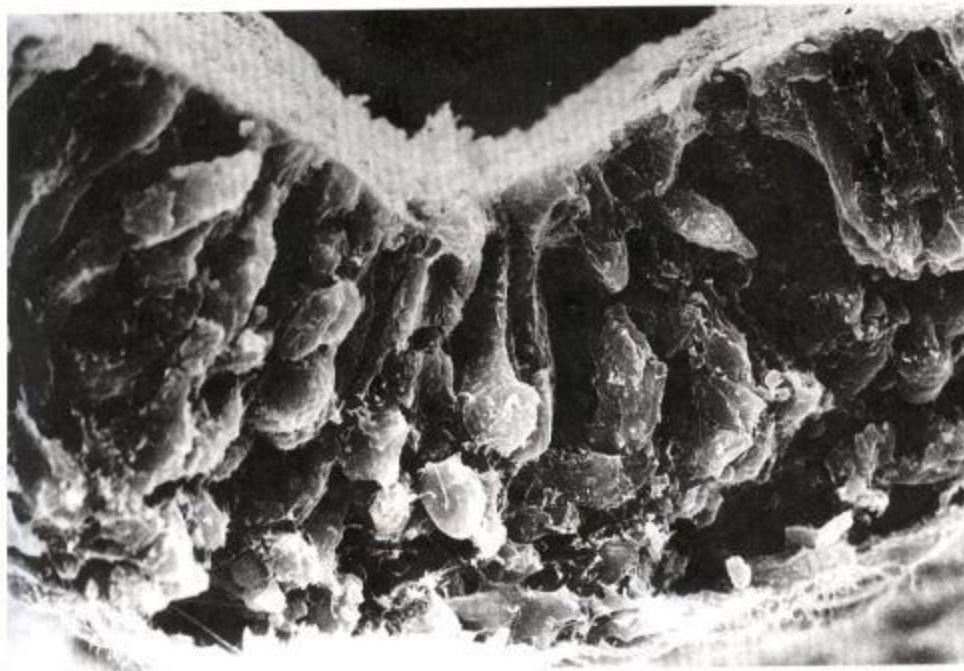
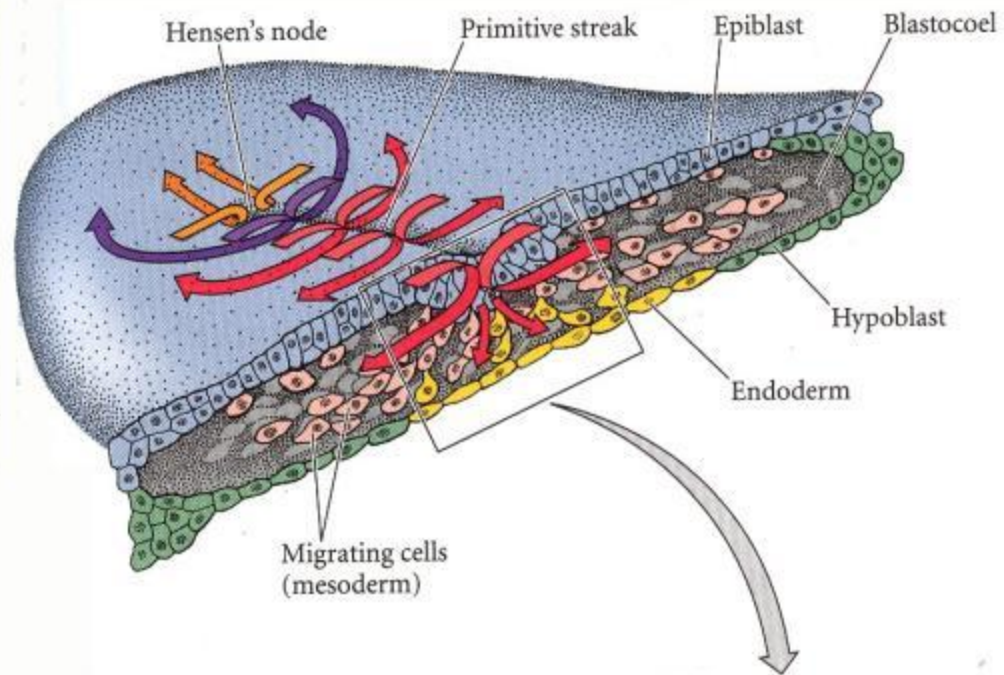


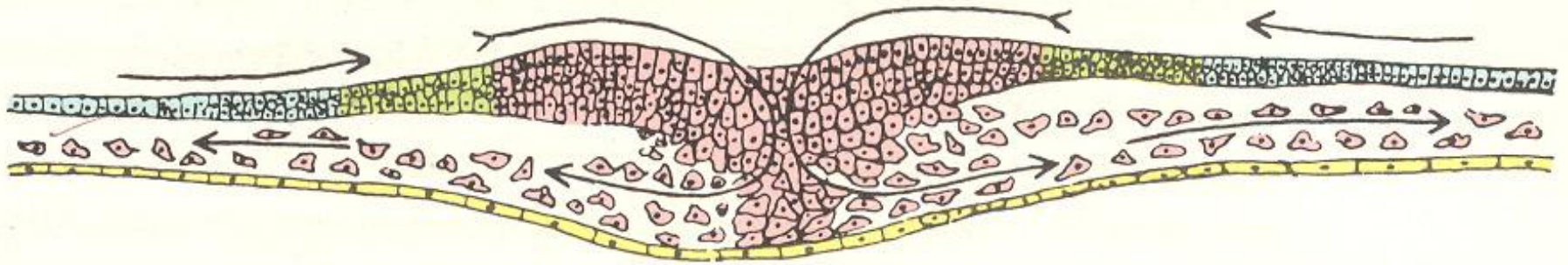
PRIMITIVE STREAK

On the surface of the epiblast there forms a thickened line of prospective mesoderm called the **PRIMITIVE STREAK**. The primitive streak lies in the longitudinal axis.

Soon, cells begin to involute along this line and the spread laterally in-between the upper and lower margins.

A groove, the **PRIMITIVE GROOVE** appears along the upper surface of the primitive streak.





A cross section of the primitive streak at the stage shown in Figures 70 I and 73 B. Mesoderm, as indicated by arrows, is rolling medially, downward in the primitive streak, and then outward laterally on either side; above, the presumptive neural ectoderm is moving inward toward the midline. (After R. Bellairs, in Marshall, *Biology and Comparative Physiology of Birds*, Academic Press.)

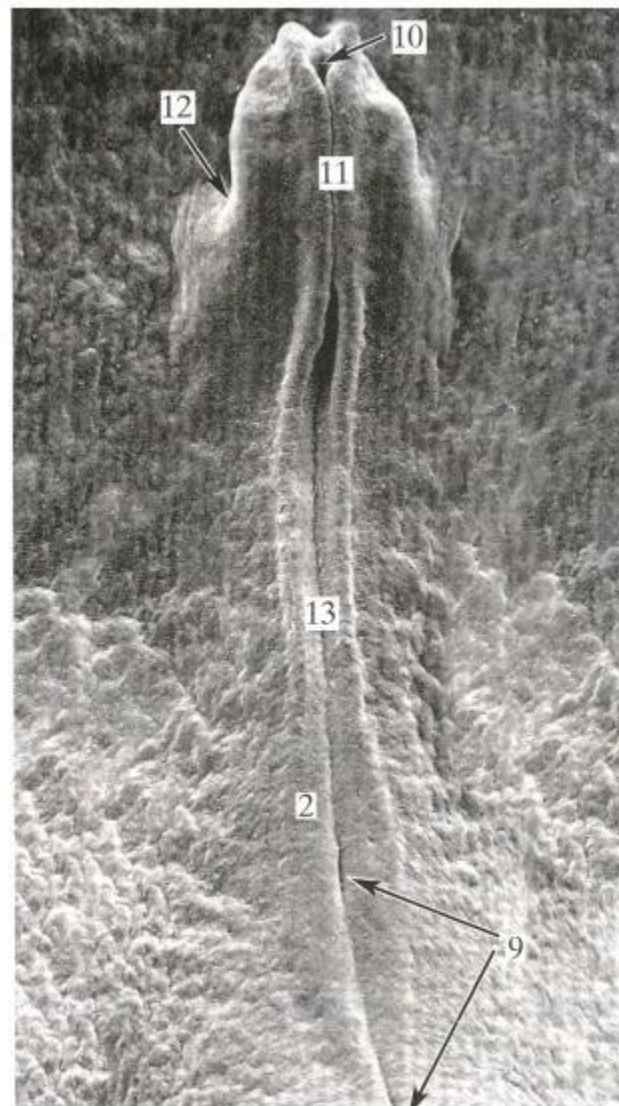
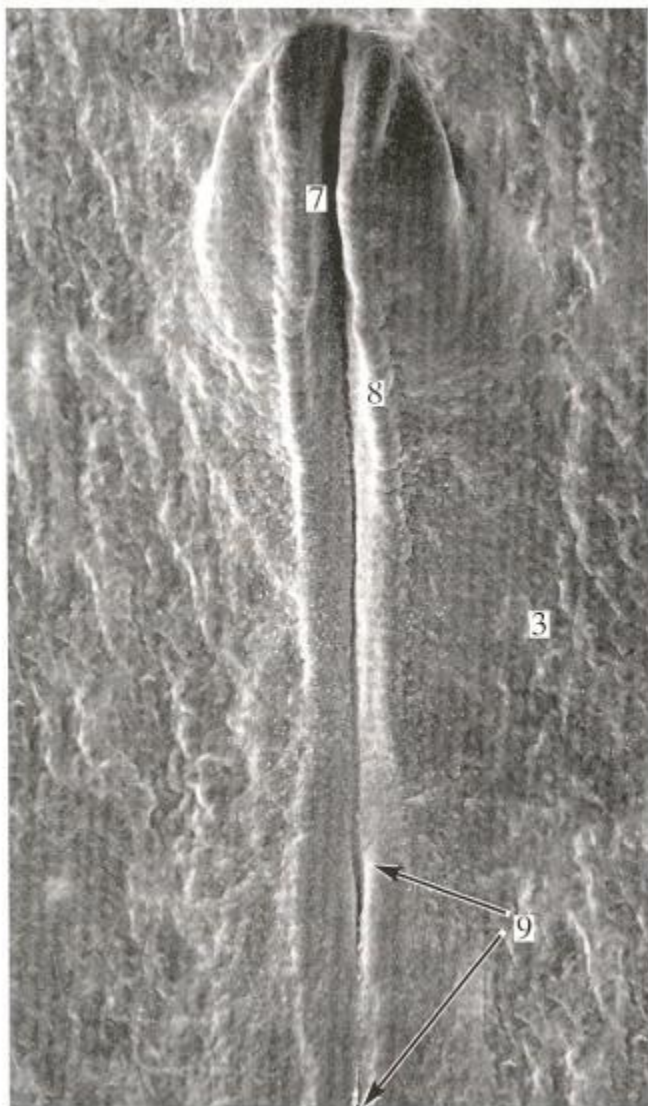
With the involution of the mesoderm, a trilaminar embryo has been achieved.

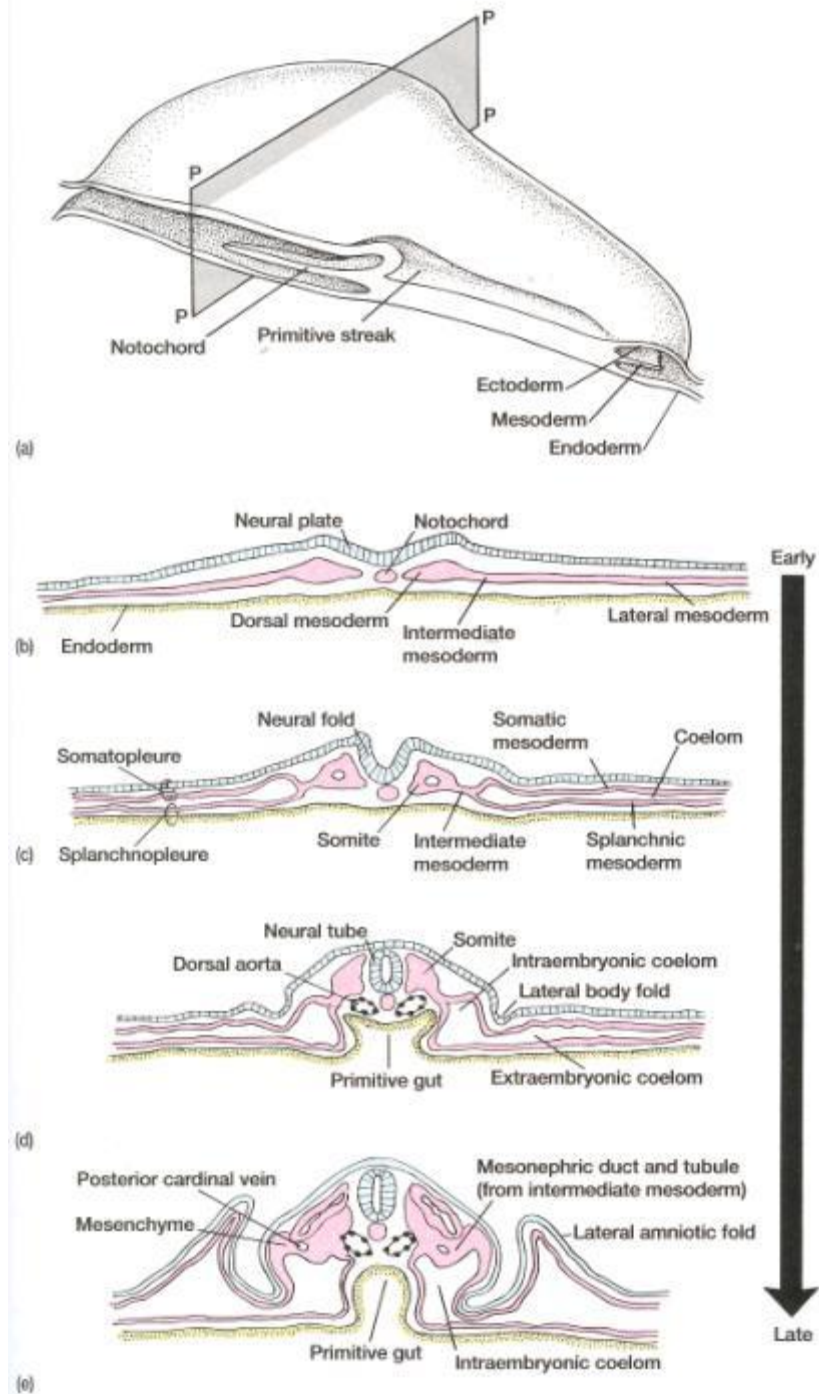
NEURULATION

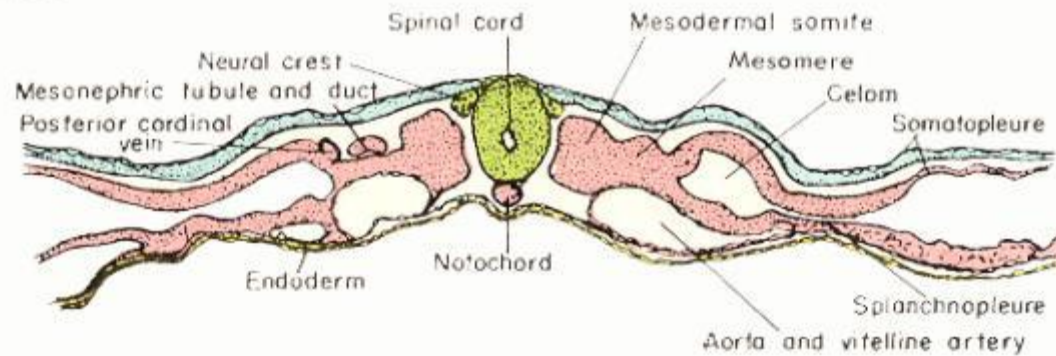
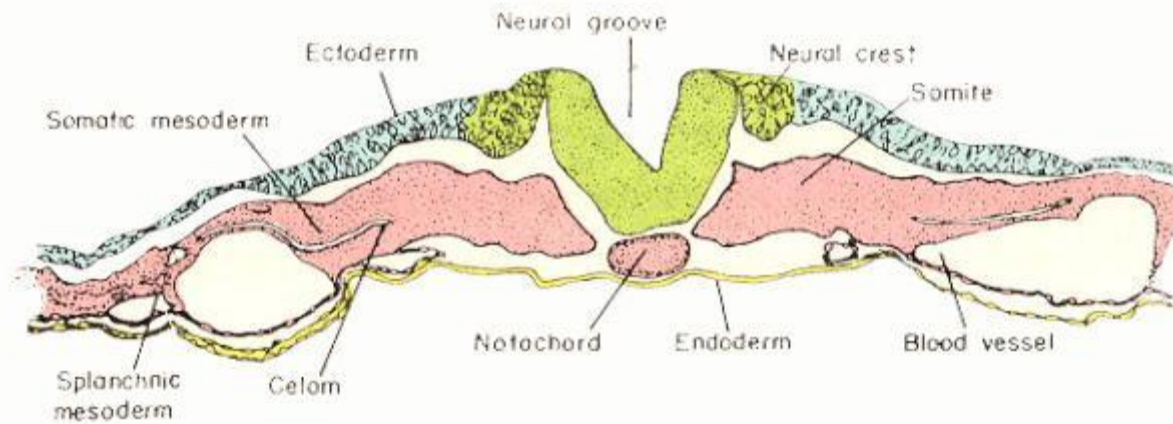
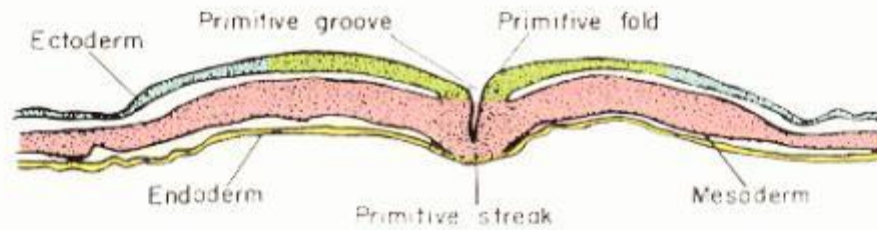
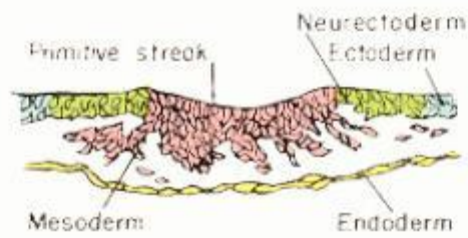
In the next stage, the involution of mesoderm is complete and the neural ectoderm has now moved in to the position of the midline. With the movement of the neural ectoderm into the midline, the NEURAL GROOVE appears.

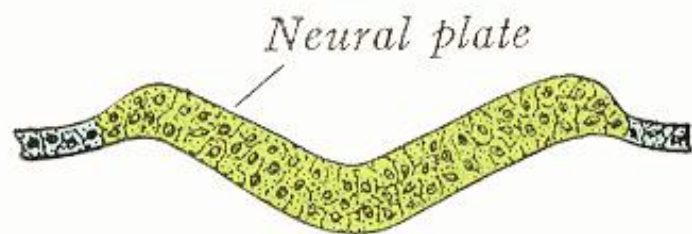
Furthermore, the mesoderm has begun to differentiate into clearly notochordal structures and LATERAL PLATE MESODERM.

Illustrate neural groove here:

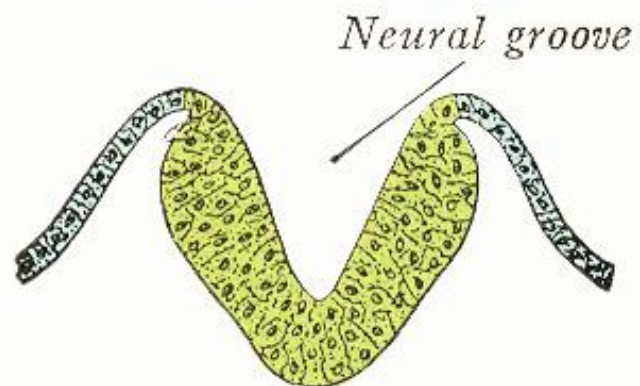




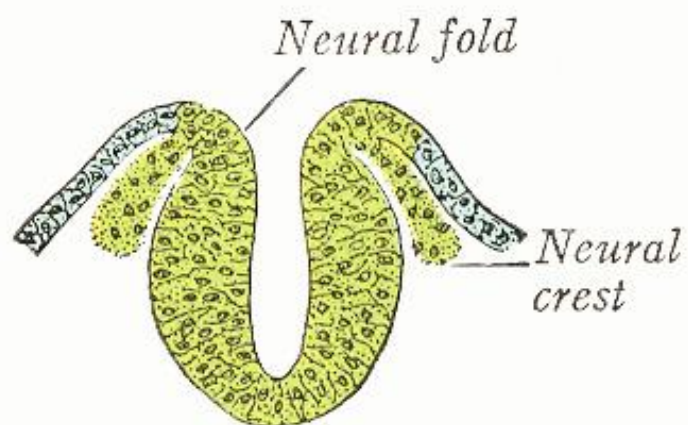




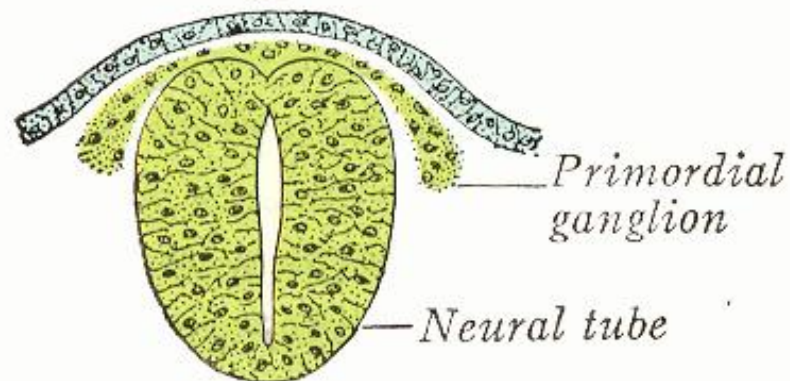
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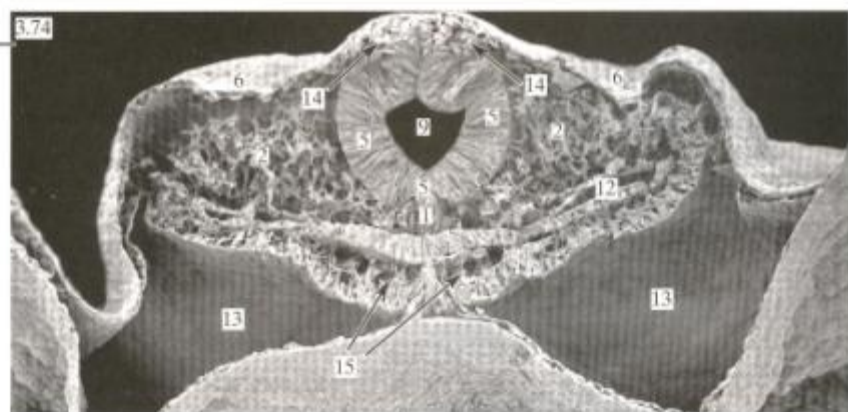
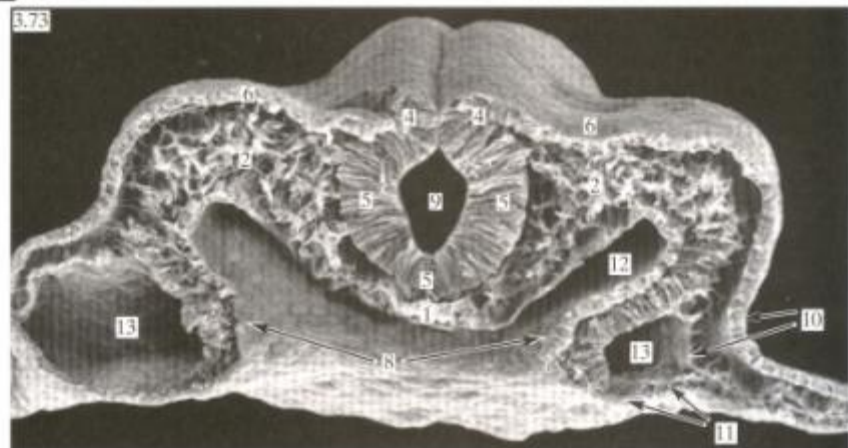
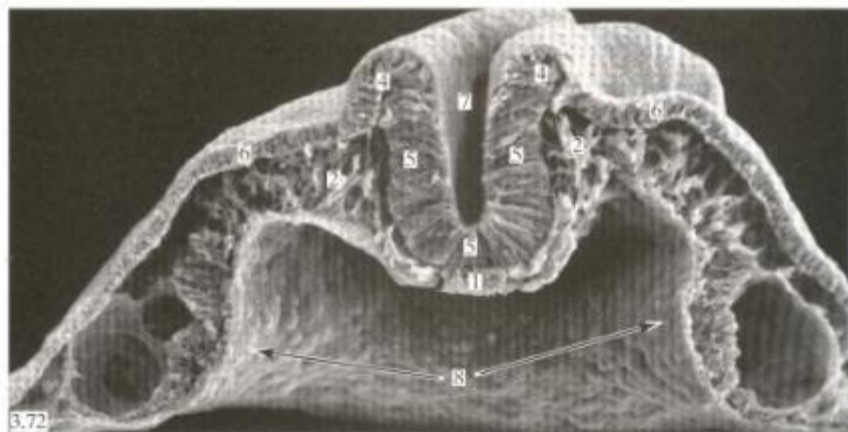
B



C



D



Illustrate “flattened cross-section here:

EXTRA-EMBRYONIC MEMBRANES

It is important to understand that only a portion of what has been diagrammed here may be called the embryo proper. The rest is “extra-embryonic”.

At this stage we have come very close to the degree of organization we saw in amphioxus and amphibians. However, we have to “zoom out” from only the embryo proper at this point to study the development and function of important structures found only in amniotes.

These are specific embryonic adaptations called **EXTRAMEBRYONIC MEMBRANES**:

1. **YOLK SAC**
2. **ALLANTOIS**
3. **AMNION** (for which the group is named)
4. **CHORION**

In the last diagram it was noted that the coelom spread out laterally beyond the embryo proper. To put it another way, the somatopleure and splanchnopleure exist as entities not only within the embryo proper, but beyond it as well.

Conventions:

For the sake of simplicity, the embryo here is simplified as a simple trilaminar structure composed of ectoderm (above) mesoderm, and endoderm (below)

Illustrate Sagittal section here:

In actuality, the extra-embryonic coelom is in continuity with the intra-embryonic coelom. It's just that the scale of our view does not allow us to visualize this.

At this point, the extra-embryonic coelom is coming to surround the yolk. This is the beginning of the **YOLK SAC**.

Although the gut is broadly open to the yolk sac at this stage, and even remains connected to the yolk via channel, we must note that food materials do not pass directly to the embryo in this manner.

Instead, the yolk sac membrane comes to be thrown into many folds. Blood vessels formed from the mesoderm associated with the extra-embryonic coelom are amongst the first circulatory structures formed. These carry food supplies to the embryo. These vessels are called **VITELLINE VEINS**.

Illustrate yolk sac and allantois here:

A few other things are happening at this stage:

1. The connection of the gut with the yolk sac has been narrowed to a yolk stalk.
2. Below the endodermal, mesodermal, and ectodermal components become continuous with one another.
3. Above, the somatopleuric folds are coming to surround the embryo.

AMNION FORMATION

Draw an illustration of the developing amnion (part I) here:

Draw an illustration of the developing amnion (part II) here:

With fusion of the somatopleuric folds, the amnion, with its fluid-filled cavity, comes to be formed. **THIS IS THE DEFINING FEATURE TO THE GREAT GROUP OF AMNIOTA (Reptiles+Birds, Mammals).**

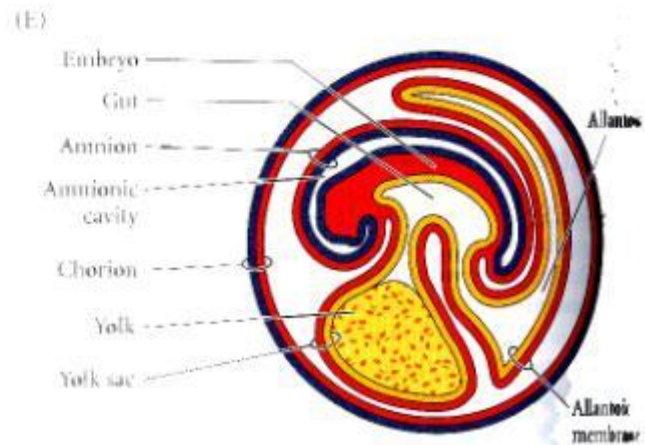
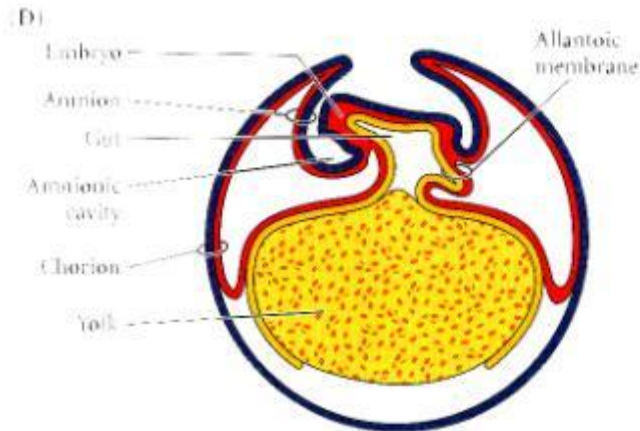
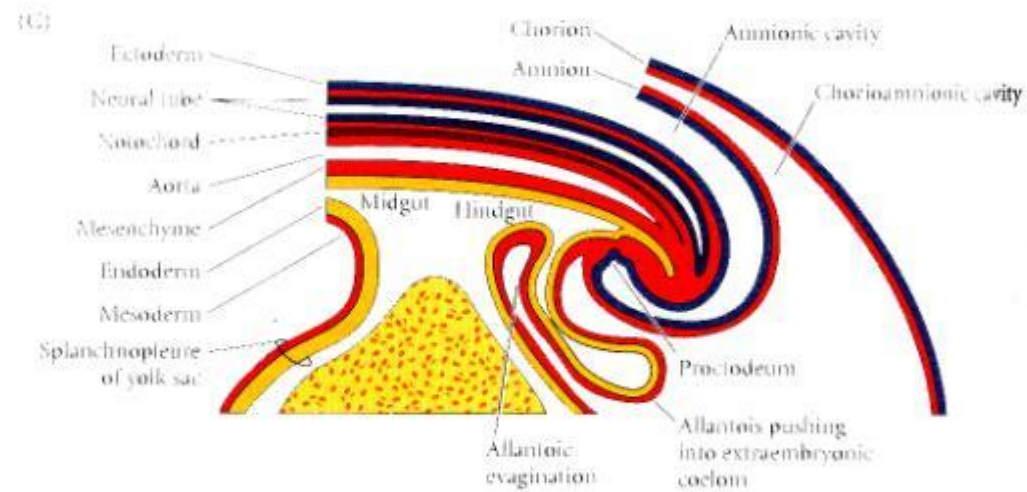
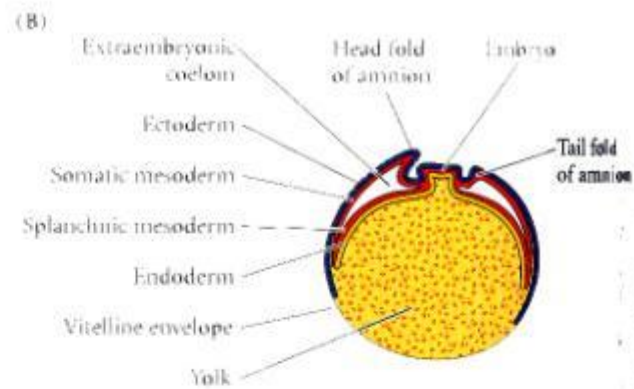
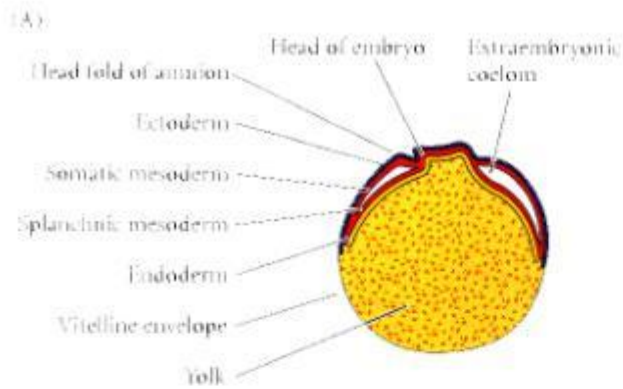
MORE ON THE AMNION:

Mesoderm contributes muscle fibers to the amnion.

The amnion secretes fluid itself to maintain its fluid-filled nature.

Amnion function:

1. Protect embryo from adhering to other membranes.
2. Protect embryo from shock / mechanical insult.
3. Prevent desiccation (originally considered to be original function, but that may not be correct.)



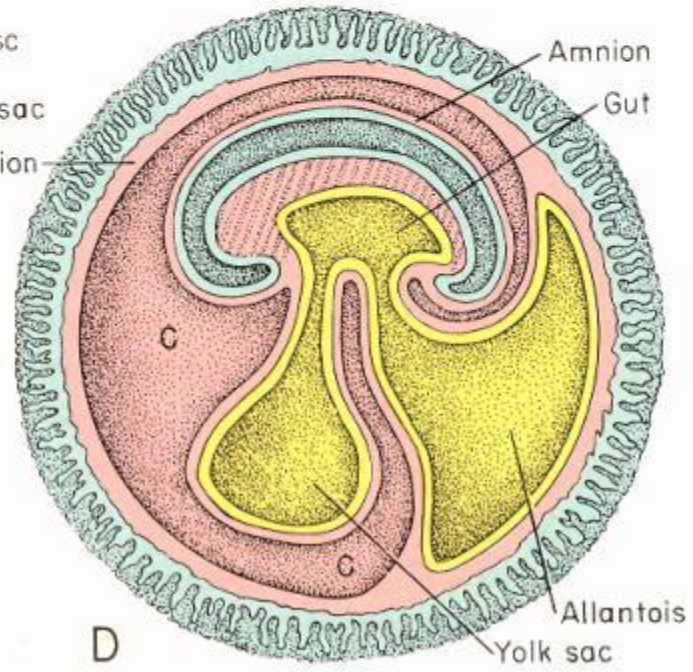
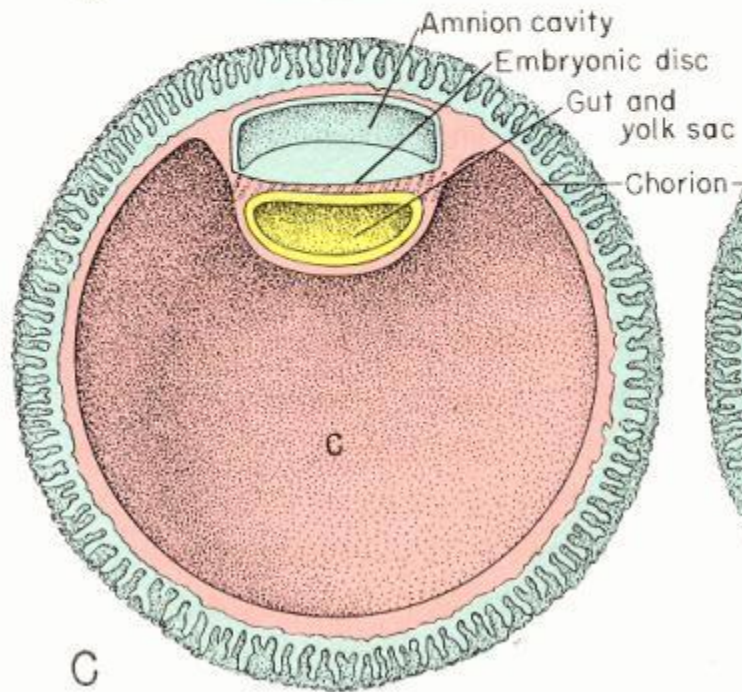
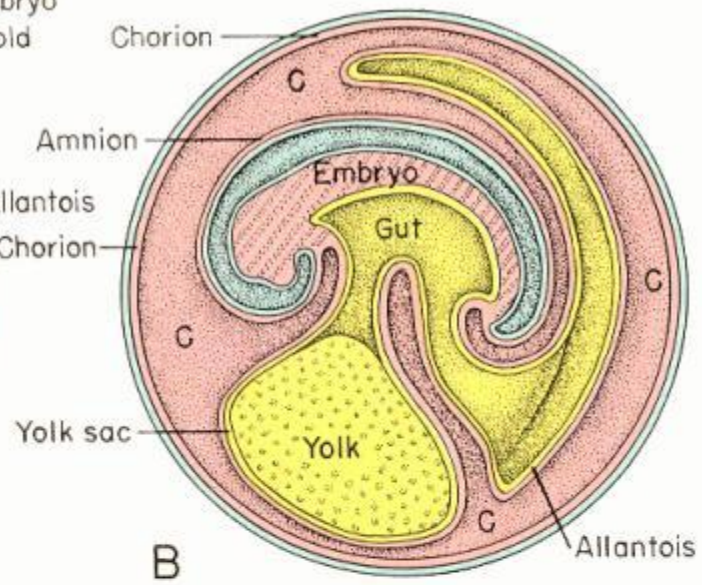
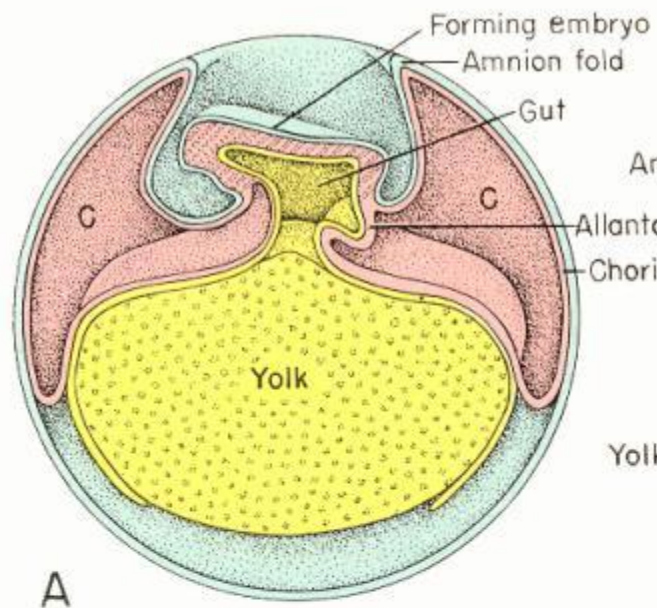
FURTHER DEVELOPMENT OF THE EXTRA-EMBRYONIC MEMBRANES

At this time the yolk stalk has become much restricted.

The allantois has become very large. It is pushing into the space of the extra-embryonic coelom.

The allantois is the embryonic refuse disposal sac. With growth and metabolic processes, waste products are generated (urea, later uric acid, others). They get dumped into the allantois. Thus, it can become quite large. It can become so large as to be seen reaching around to the front side of the diagram.

Illustrate further development of allantois here:



THE CHORION AND CHORIO-ALLANTOIC MEMBRANE.

The portion of the extra-embryonic coelom that has not contributed to the formation of the amnion is the **CHORION**.

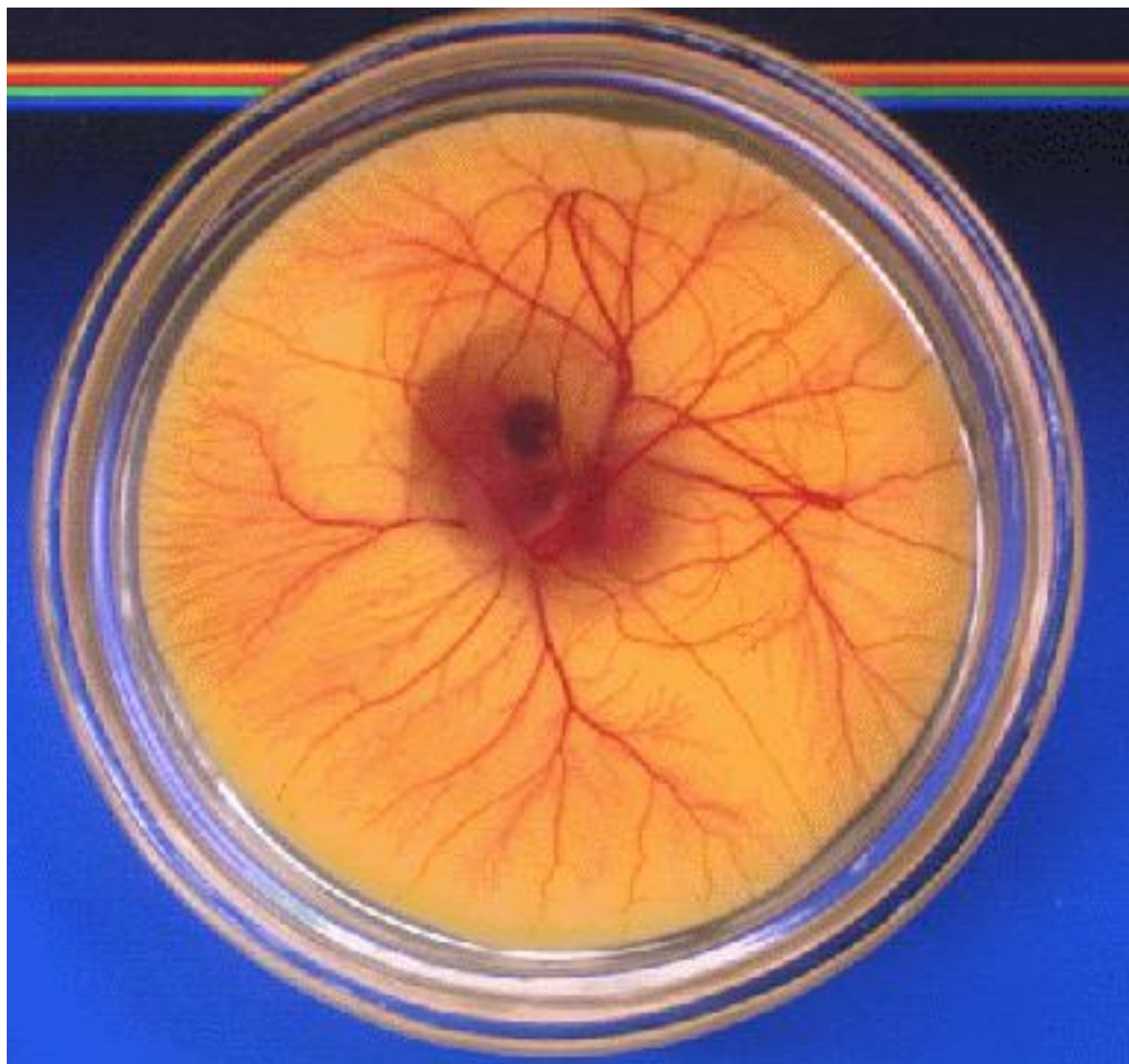
Eventually, the allantois continues to grow so large that its outer mesodermal layer comes into contact with the inner mesodermal layer of the chorion.

As they come into contact (as with most cases when like tissue touches like tissue) the mesodermal components fuse. This creates a compound membrane formed of all three germ layers: the **CHORIO-ALLANTOIC MEMBRANE**.

The chorio-allantoic membrane performs an important function in reptiles and birds and the truly terrestrial existence. The membrane comes to lie up against the egg shell.

Blood vessels form from the mesoderm. It is through the chorio-allantoic membrane that the organism respire. Blood vessels of the allantois carry carbon-dioxide toward the chorio-allantoic membrane and oxygen away from it.

Illustrate the chorio-allantoic membrane here:



FURTHER DEVELOPMENT OF THE INTRA-EMBRYONIC BODY STRUCTURES

(Recall that the gut is open ventrally at this point.)

The lateral folds (as well as the head and tail folds) push farther down and underneath the embryo proper.

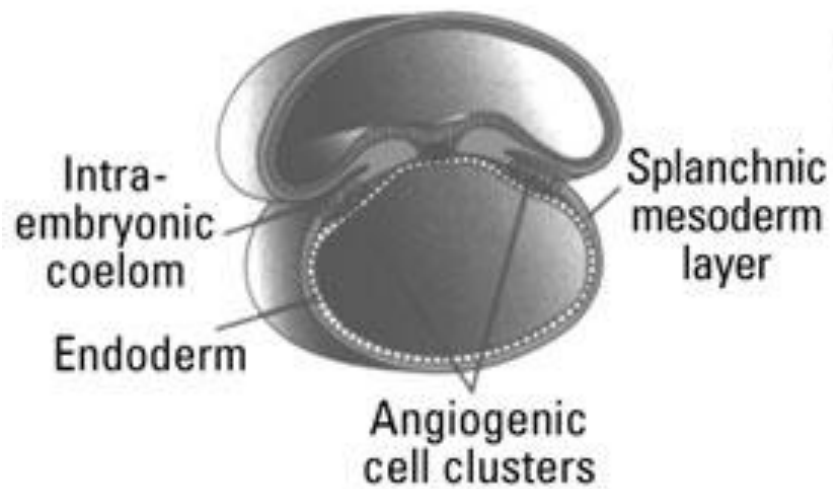
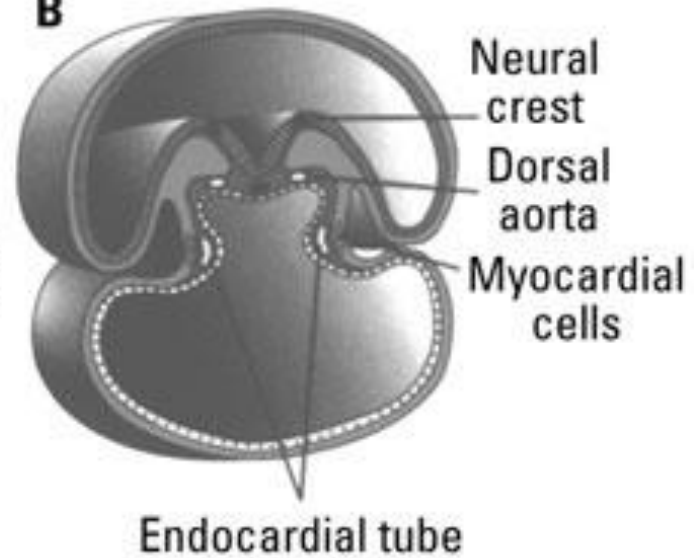
Illustrate pinching of the lateral folds here:

The mesodermal pouches of the intra-embryonic coelom are pinched off from the extra-embryonic coelom, as is the gut cavity.

Illustrate pinched off coelom here:

Finally, the ventral ectodermal folds come to meet in the ventral midline.

Illustrate a basic cross-section here:

A**B****C**