

***Biology 340***  
***Comparative Embryology***  
***Lecture 9***  
***Dr. Stuart Sumida***

# Introduction to Early Mammalian Development

If we were to turn directly to the early ontogeny of placental mammals, we would see rather large and fundamental differences from the picture we have gained of the basal amniote condition as modeled by reptiles/birds.

We can make the more easily and less abruptly if we consider the phylogenetic context of all mammals, and included all groups of extant mammals:

## MAMMALIA

**Prototheria** - the egg laying mammals, currently restricted in a relict distribution in Australia and New Guinea (the platypus and echidna)

**Theria** - mammals with internal development

**Metatheria** - the marsupials (pouched mammals) in which the young leave the womb in a very premature stage to complete their development in an external pouch

**Eutheria** - the placental mammals in which young are born in a more fully developed state.

## PROTOTHERIANS

In the living prototherians (platypus and echidna), the size of the total “egg”, including the external envelopes of albumen and the leathery shell is about 15 mm in diameter. Of this, the egg proper is about 5 mm. Though smaller than in birds, this is enormous compared to the eggs of therians.

As in reptiles and birds, the egg is MACROLECITHAL, and cleavage is meroblastic. Further, as in reptile and birds, the embryo proper develops from a restricted blastodisc. Given the clearly primitive nature of prototherians, we see here the “macrolecithal ancestry” of mammals.

In therian mammals (both marsupials and placentals) the eggs are very small.

- Placentals: range from 0.1 - 0.2 mm. (Humans ~0.15 mm)
- Marsupials: exhibit a greater range of sizes.

Importantly, in both groups, the eggs are MICROLECITHAL and cleavage is HOLOBLASTIC.

Despite the macrolecithal nature of their eggs, therian mammals “betray” their macrolecithal heritage in the forming of a yolk sac - even there is little or no yolk.

The yolk sac contains almost no yolk. Instead, other provisions are made for the nourishment of the developing embryo:

A portion of the genital tract of the female is formed into a UTERUS in which the embryo develops into a more or less advanced state before birth.

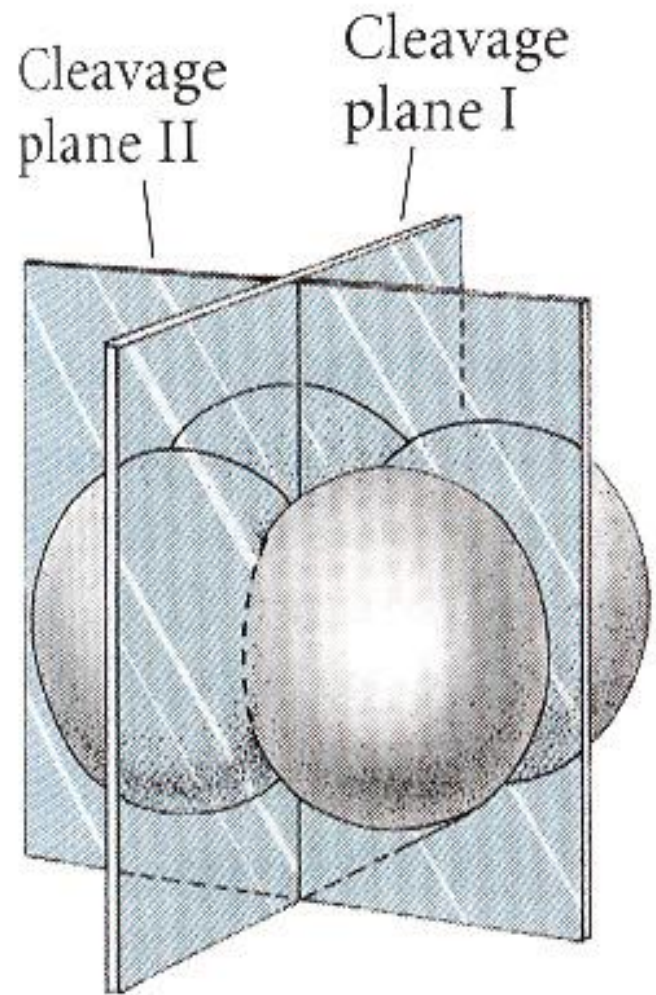
During its uterine life, the embryo absorbs food from its mother through a structure called the PLACENTA. Later we will see that it is formed through modification of the extra-embryonic membranes inherited from the macrolecithal “reptile-like” ancestors of therians.

# EARLY CLEAVAGE IN MAMMALS

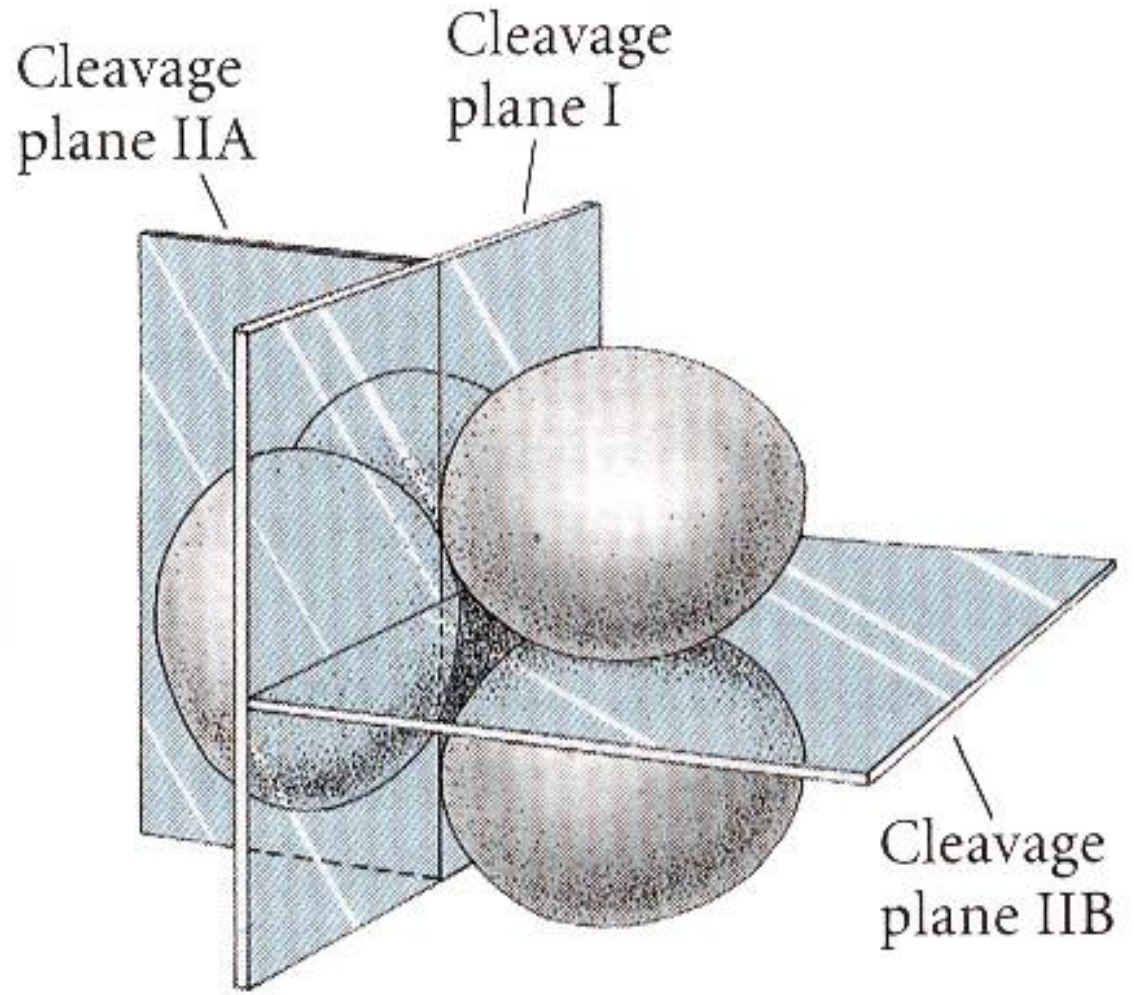
First Cleavage - takes place while embryo is still on one to the uterine tubes of the mother.

Second Cleavage: While deuterostomes, the second cleavage, is different from that of other vertebrates. Mammals have what's known as **ROTATIONAL CLEAVAGE** wherein one of the blastomeres divides meridianally, and the other equatorially.

Subsequent Cleavages are relatively less organized.

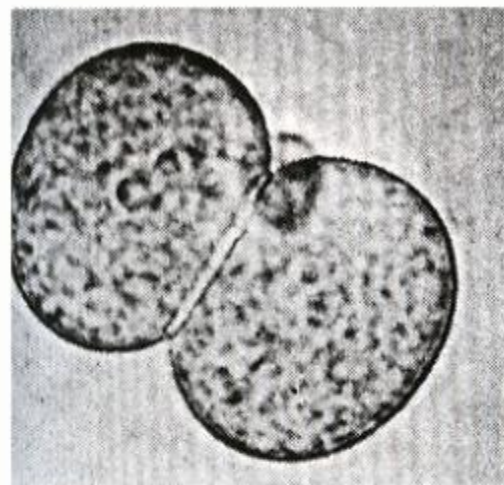


ECHINODERM  
AND AMPHIBIAN

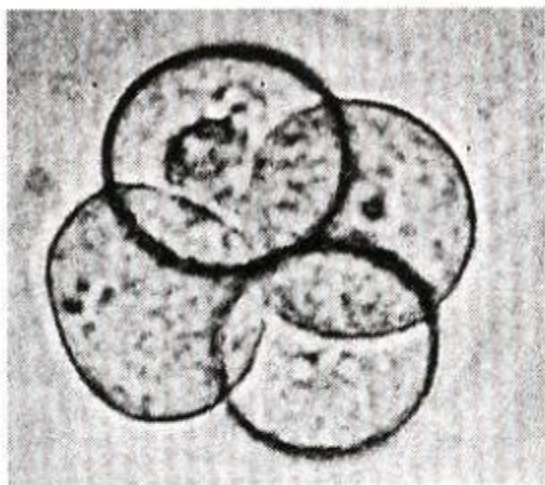


MAMMAL

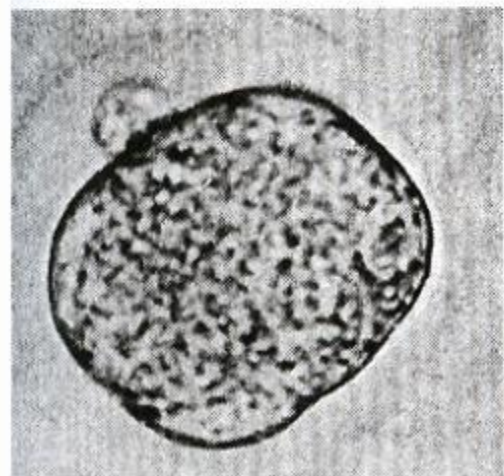
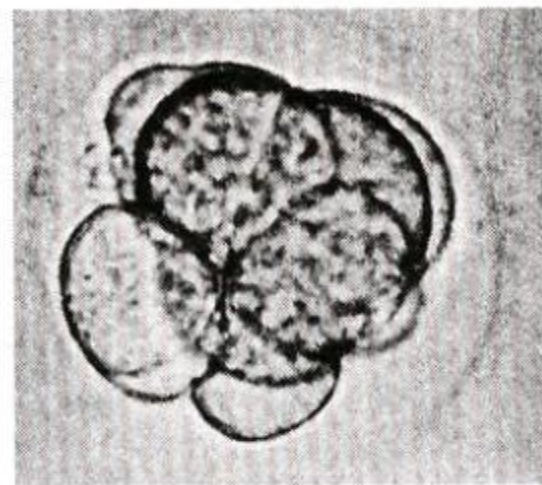




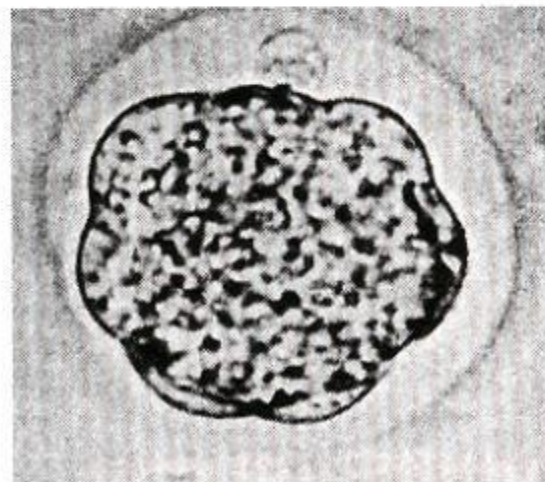
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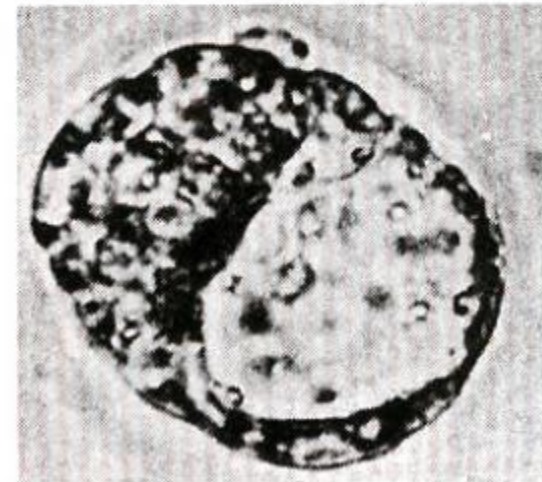
(C)



(E)



(F)





By the 16-cell stage, the developing organism has usually reached the uterus.

After awhile, a small sphere of cells is formed. It is about the size of a head of a pin, and is called the **MORULA** (mulberry).



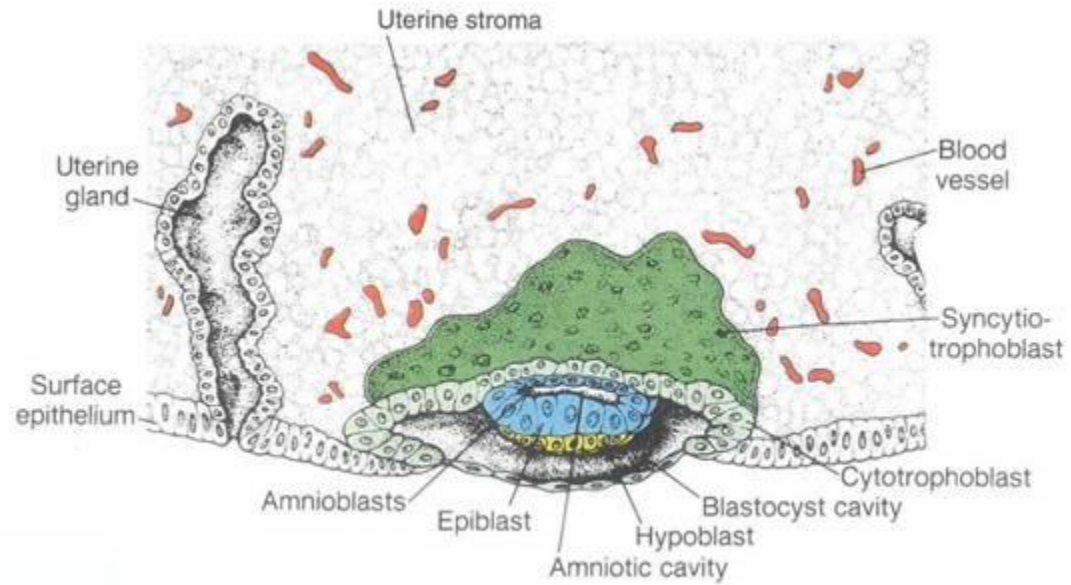
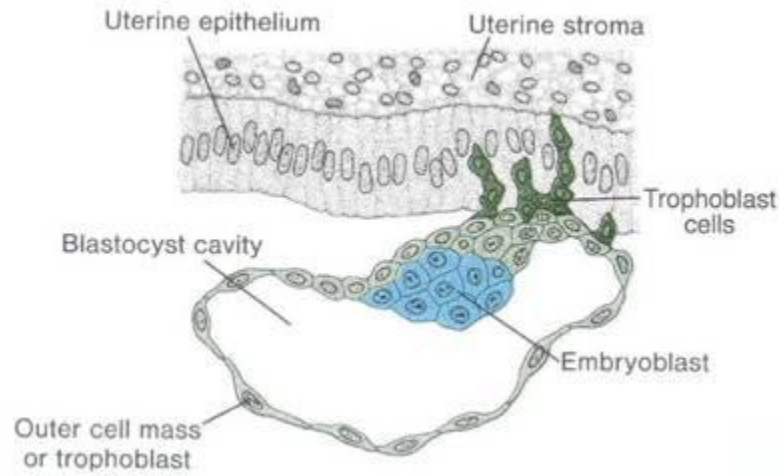
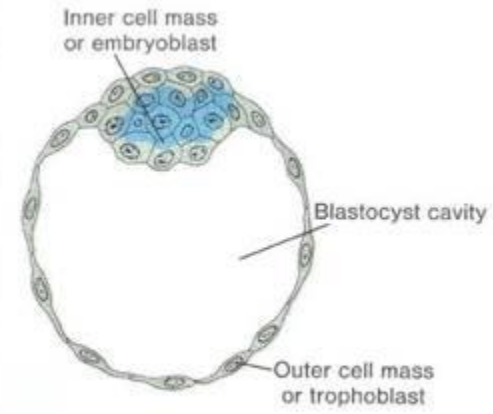
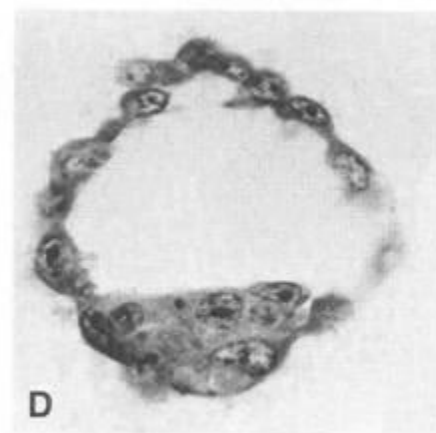
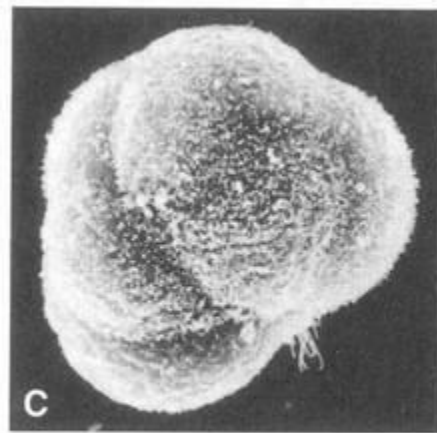
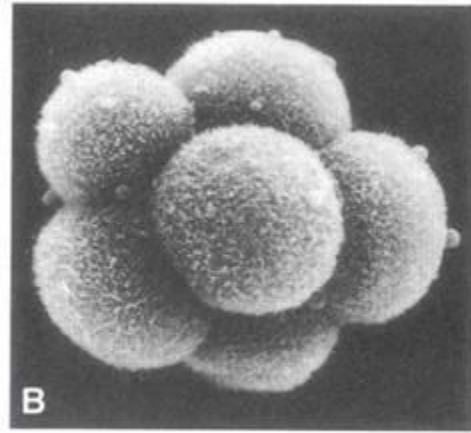
Morula

# INNER CELL MASS

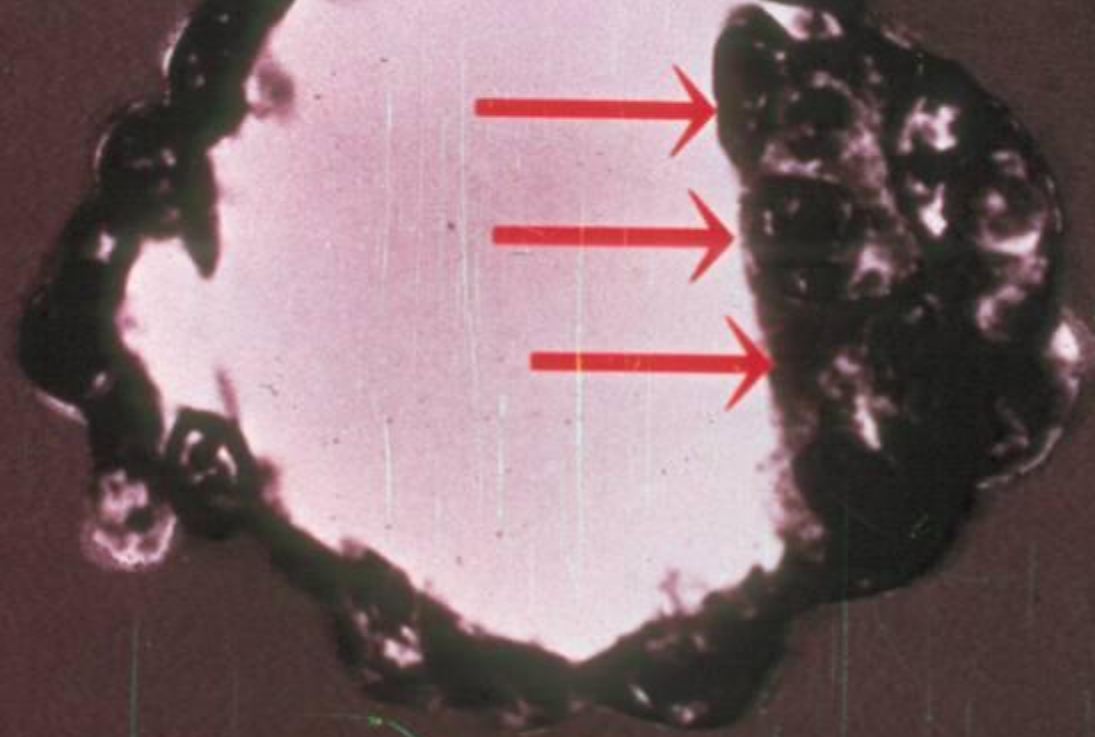
With the continued multiplication of cells, a fluid-filled cavity appears within the morula, and a cross-section would show that this cavity is eccentrically placed. At this stage, the embryo is called a **BLASTOCYST**.

The upper cluster of cells is called the **INNER CELL MASS**. It is from this that the embryo proper will develop.

The cells of the outer wall are called the **TROPHOBLAST**. They will be involved in the formation of the extra-embryonic membranes.

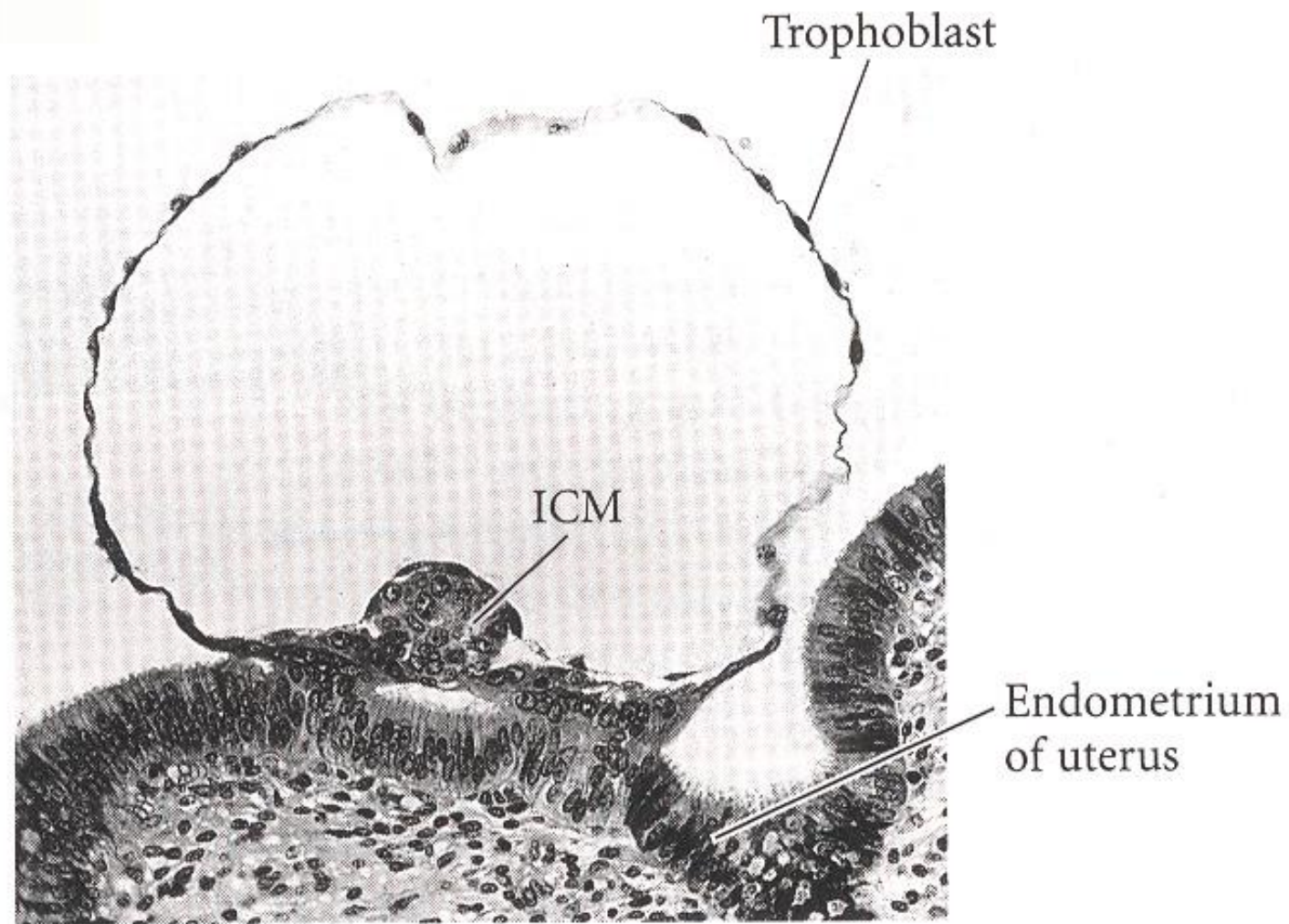


**INNER CELL MASS**

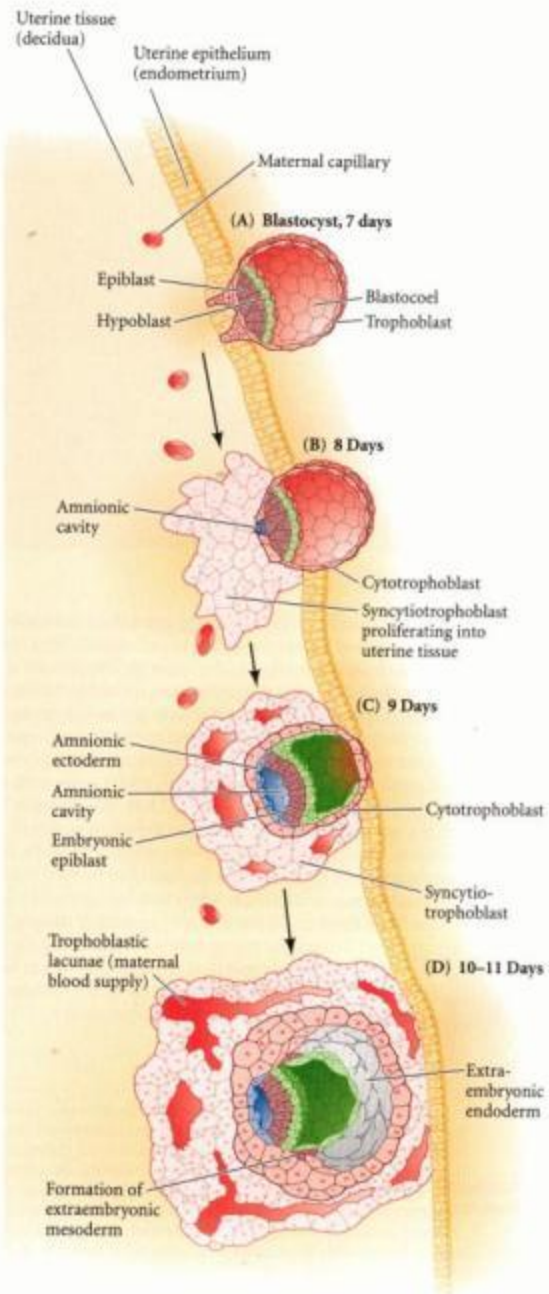


**THE GROUP OF LARGE CELLS CALLED THE "INNER CELL MASS" WILL FORM THE EMBRYO.**





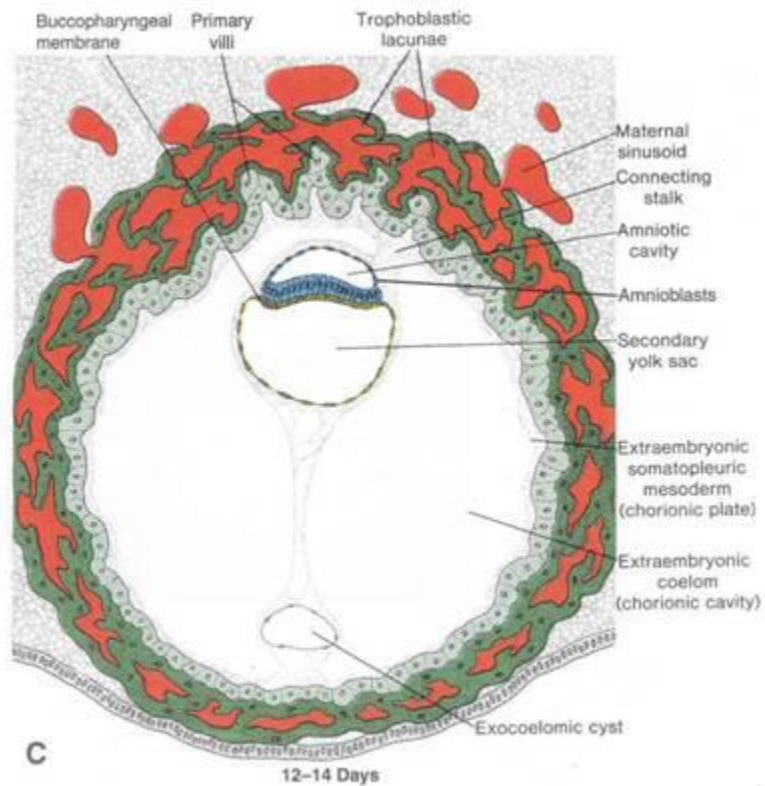
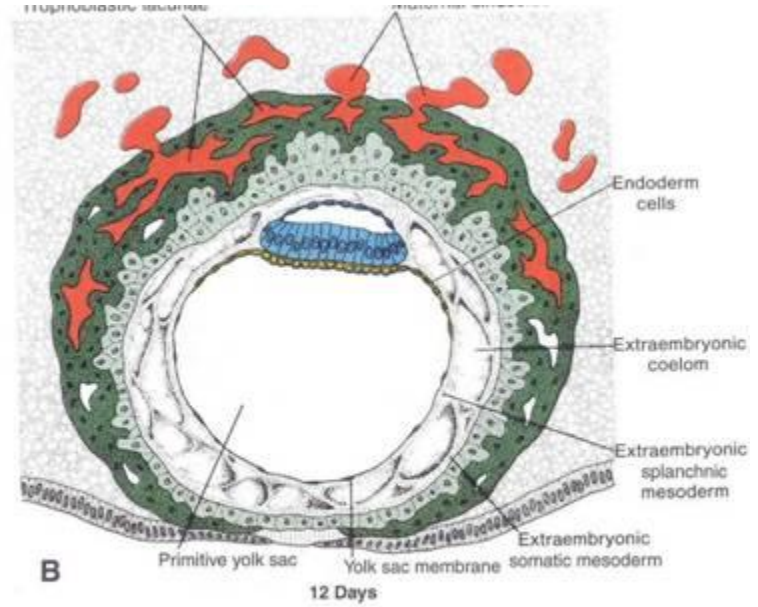
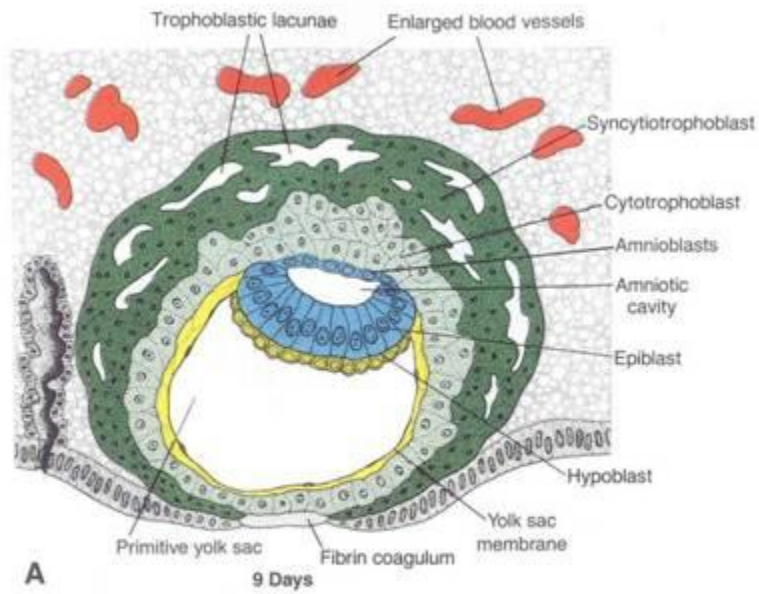




That such a stage could be derived from a reptilian ancestry is not immediately apparent. However, one must bear in mind that this phylogeny has involved a *change in ontogeny* from a macrolecithal to a macrolecithal egg - in other words, one not constrained by yolk.

Consider it this way: If you were to cut through the trophoblast and spread it out over the mass of a large yolk, it would look a lot like a macrolecithal egg.

Now, there isn't much yolk, but there is a tiny bit. Further, the cavity of the blastocyst is equivalent to the subgerminal space that underlies the blastoderm in reptiles/birds.



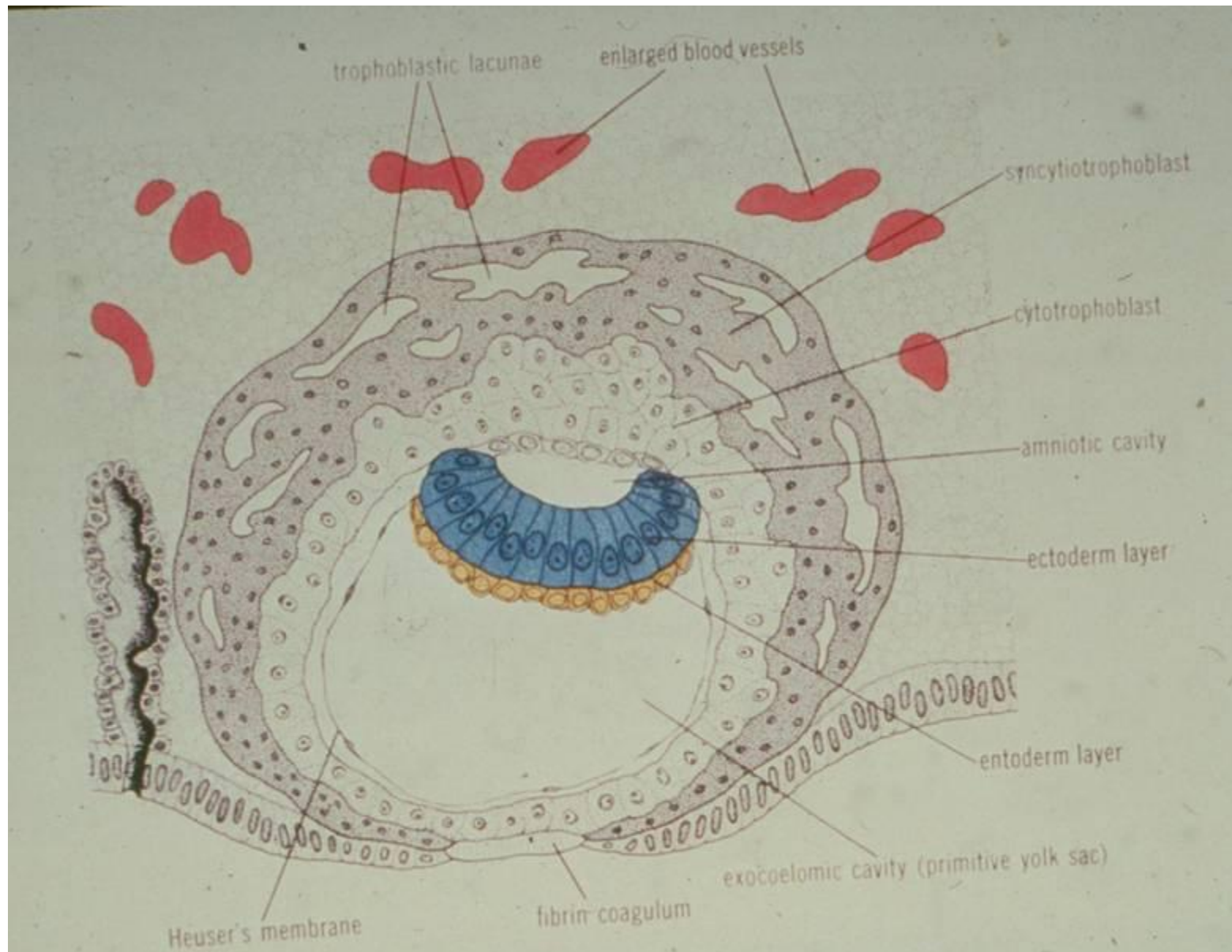
# ACCELERATED FORMATION OF THE AMNIOTIC CAVITY

Recall that in reptiles and birds, the amniotic cavity forms by a complex pattern of folding of somatopleuric folds. In mammals...instead...the amniotic cavity forms at a tremendously accelerated rate by a process known as **CAVITATION**.

First, the cells of the lowest level of the inner cell mass become grouped as a layer of **PRIMARY ENDODERM** and a space appears between the inner cell mass and the upper part of the trophoblast.

Essentially, the inner cell mass “pulls away” from the trophoblast, leaving a space that eventually becomes the amniotic cavity.

This is a distinct change in developmental timing, as the amniotic cavity is present even before the presumptive mesoderm forms.



Next, the endoderm becomes a much more extensive layer, completely lining the cavity beneath the inner cell mass.

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We may now refer to the plate of cells immediately beneath the prospective amniotic cavity as the **EPIBLAST**.

It is not entirely clear where the extra-embryonic endoderm comes from. It may be derived from the trophoblast, or it may result from a spreading of the original endoderm (or both).



Next: the cells of the extra-embryonic mesoderm differentiate from the trophoblast, coming to lie between the trophoblast and the endoderm.

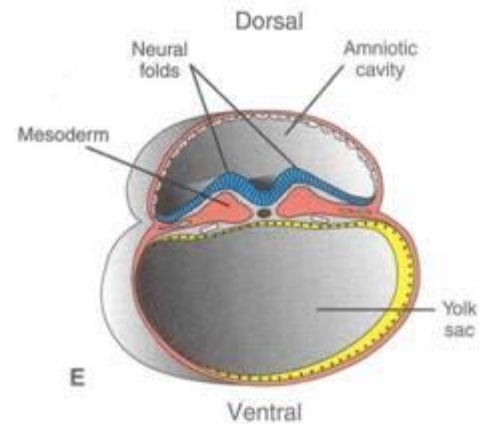
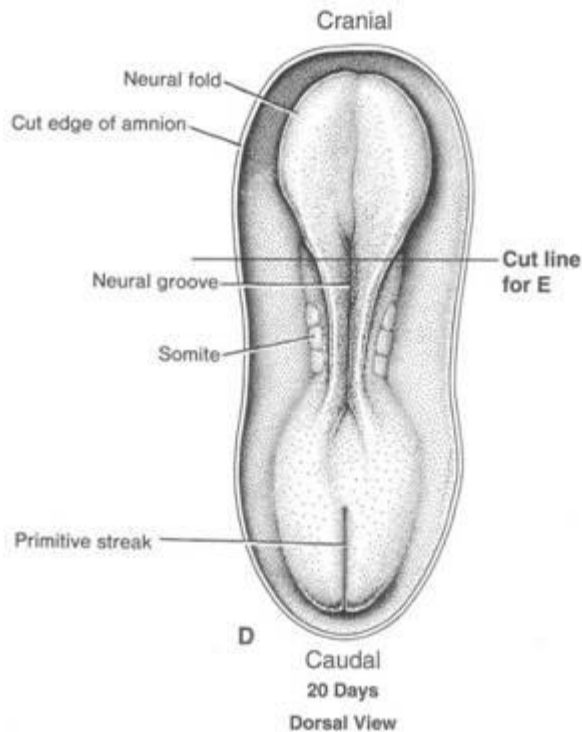
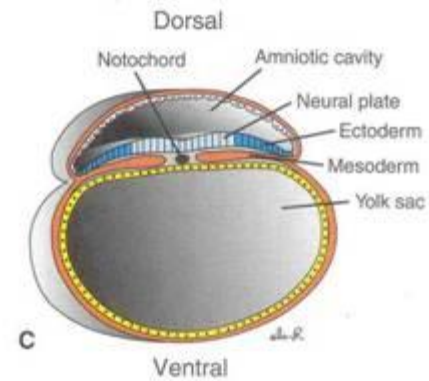
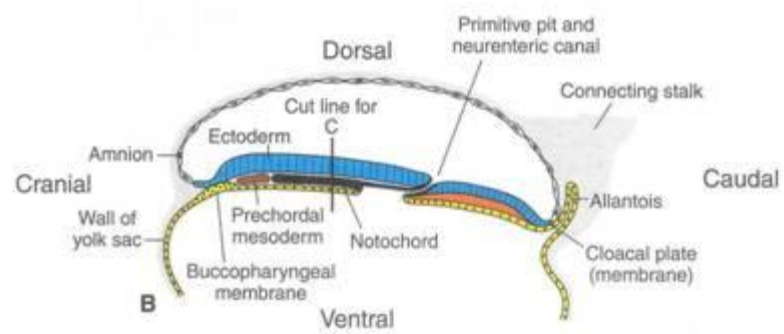
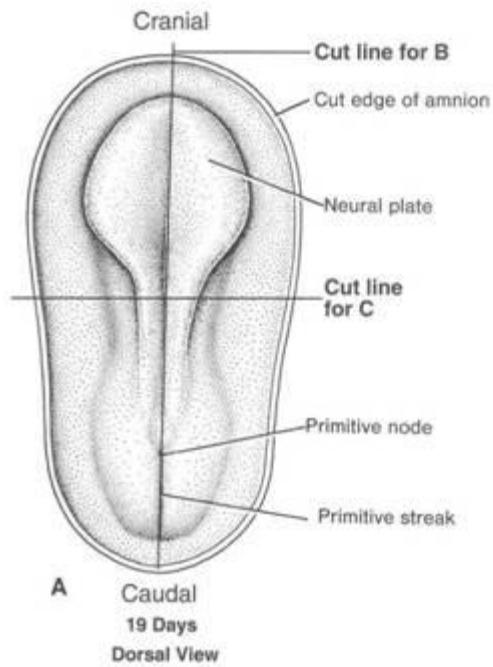
This is another change in developmental timing. The extra-embryonic mesoderm forms BEFORE the mesoderm of the embryo proper. Another example of heterochrony and acceleration.

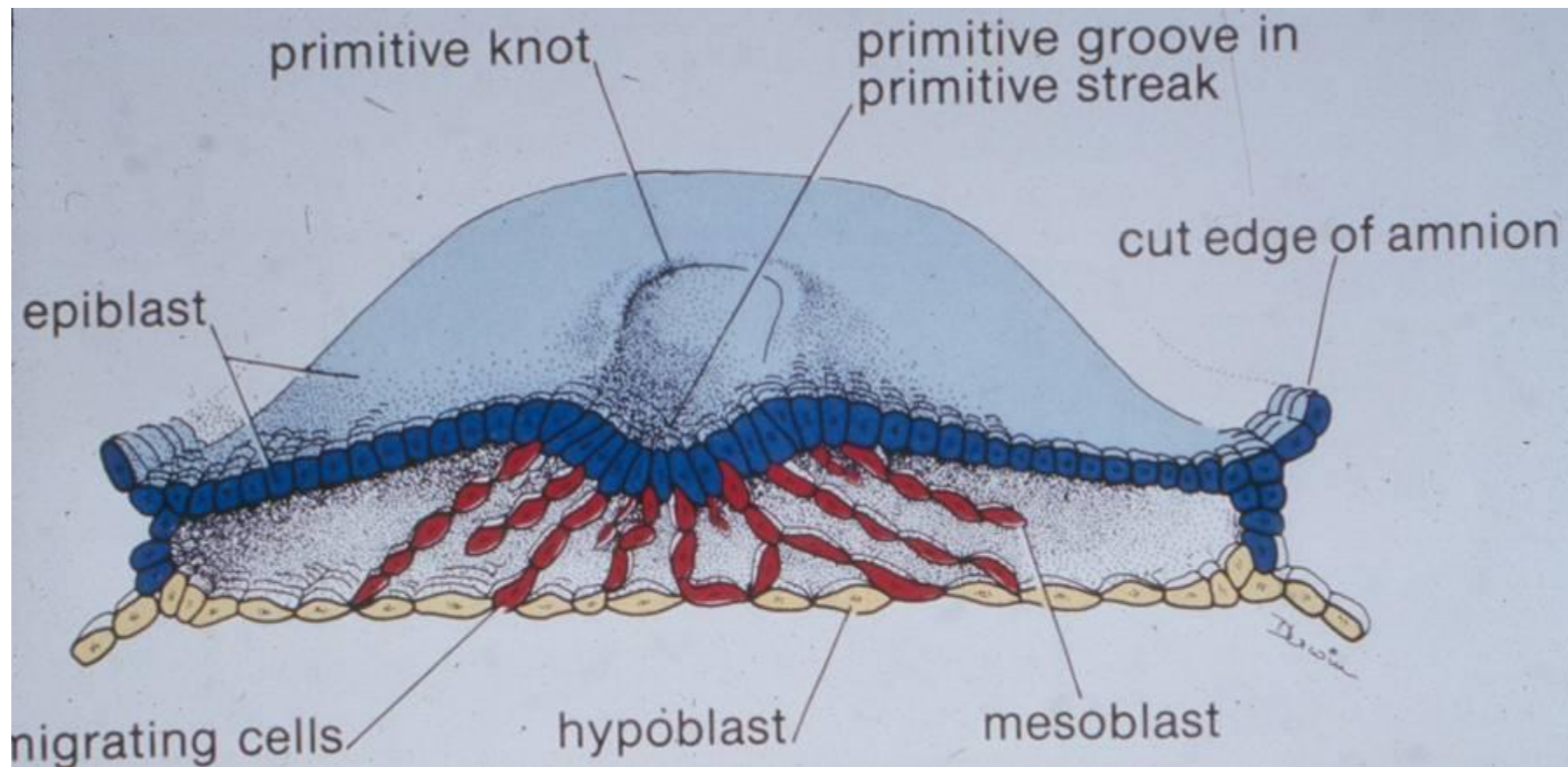
Also, now note that the remaining trophoblast corresponds to the extra-embryonic ectoderm. The stage of the trilaminar embryo has been reached extra-embryonically before it is intra-embryonically.

# FURTHER MESODERMAL DEVELOPMENT

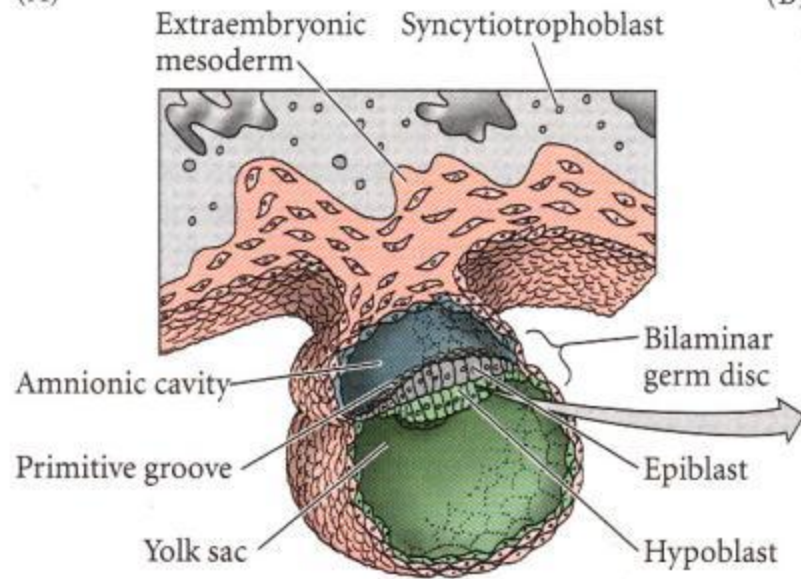
At this point, a number of things happen simultaneously:

- Spaces appear within the extra-embryonic mesoderm - forming an extra-embryonic coelom.
- Mesoderm appears in the embryo proper through a process of involution through a primitive streak - much as in (macrolecithal!) reptiles+birds.
- The intra-embryonic mesoderm comes to connect up with the extra-embryonic mesoderm.

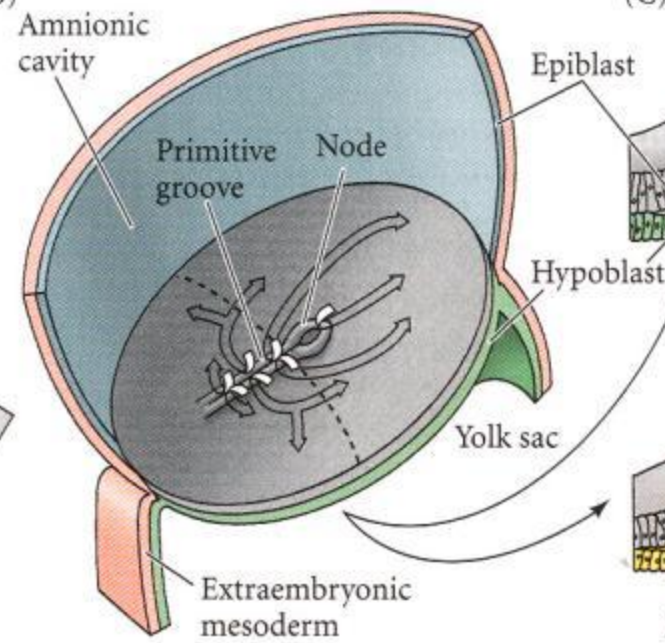




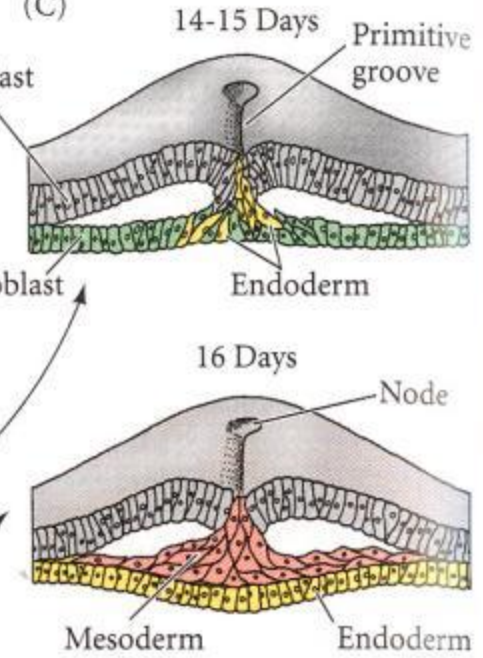
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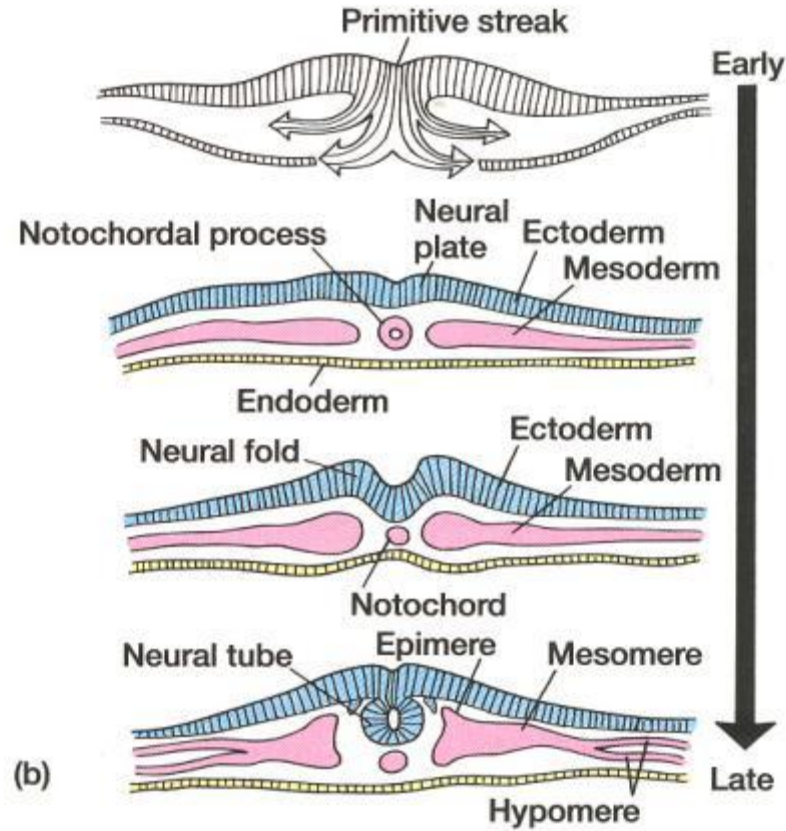
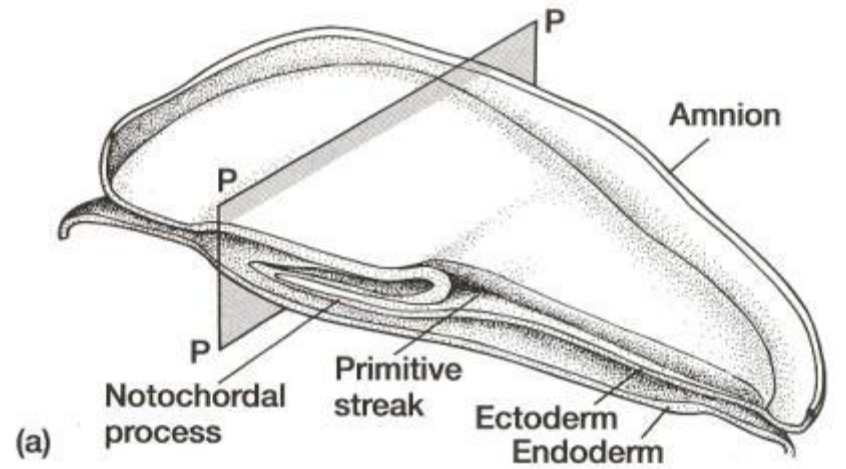
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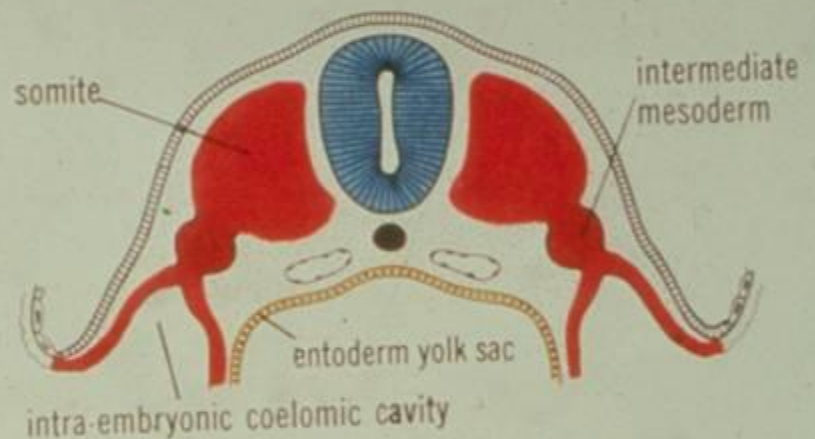
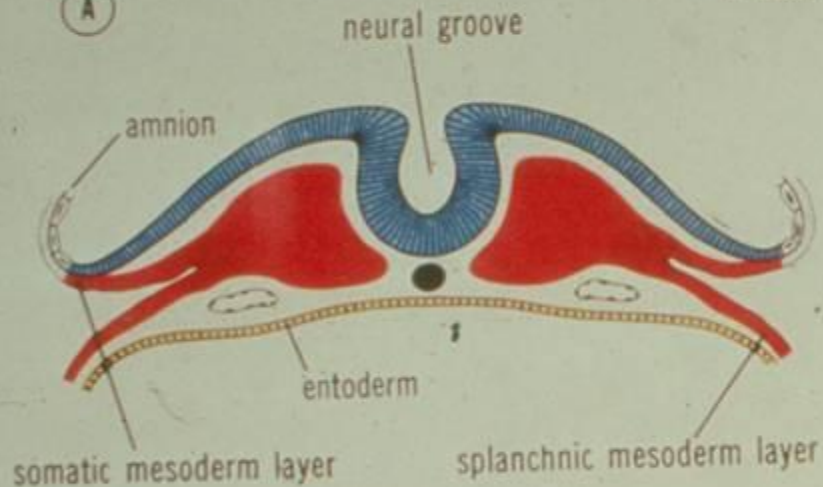
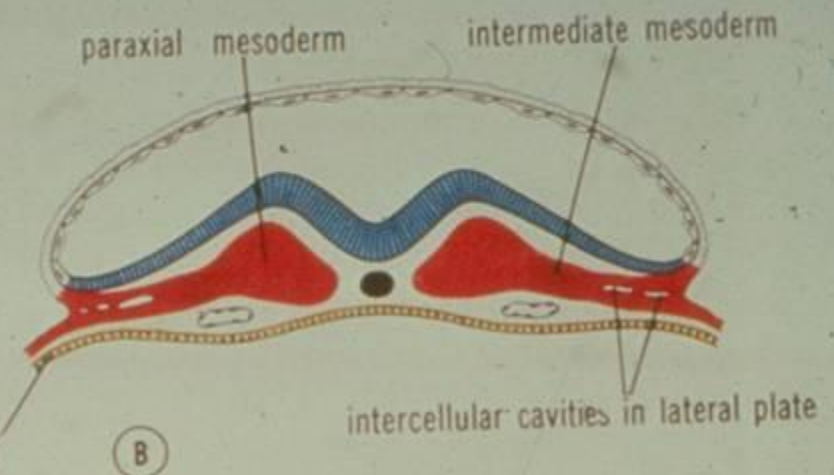
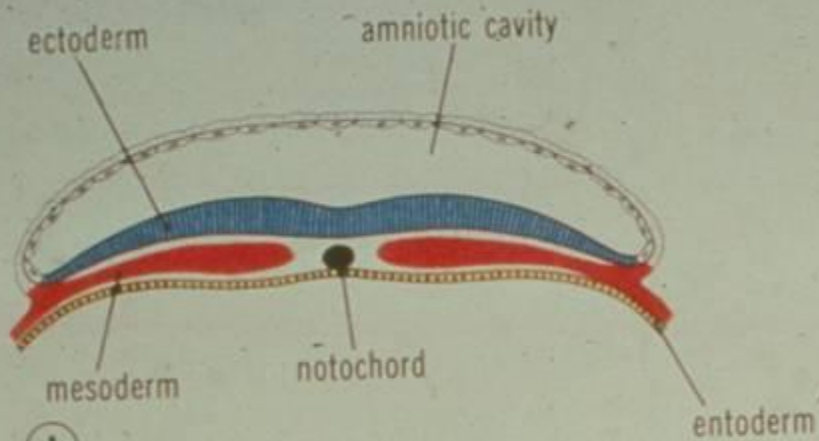
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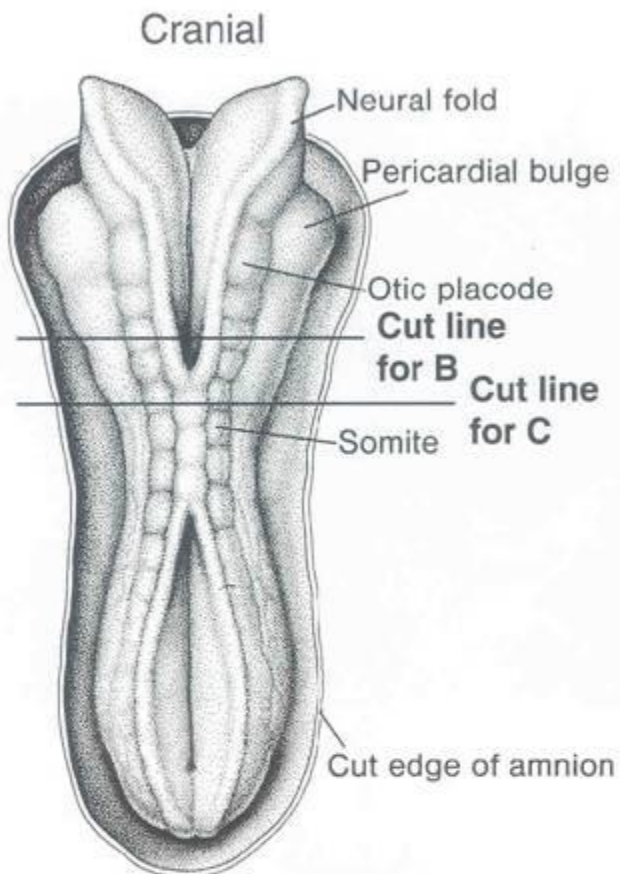




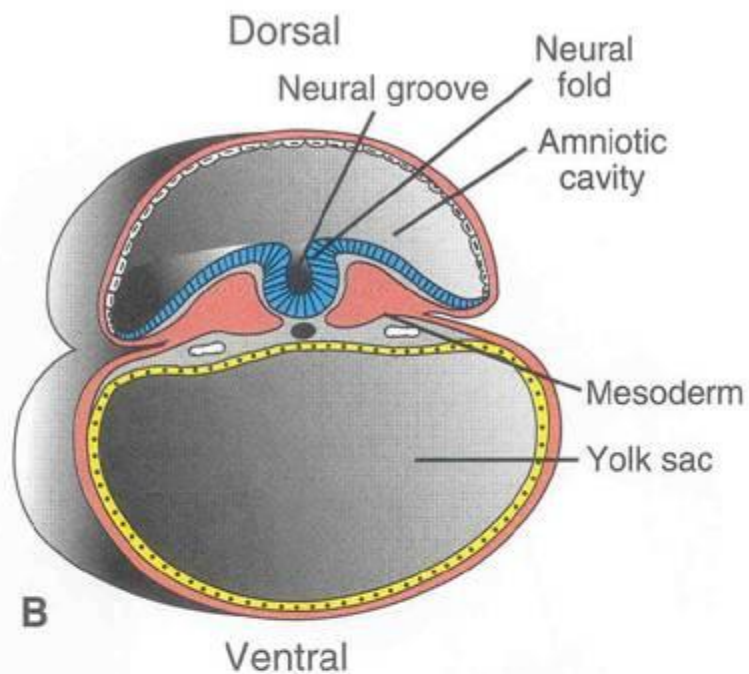




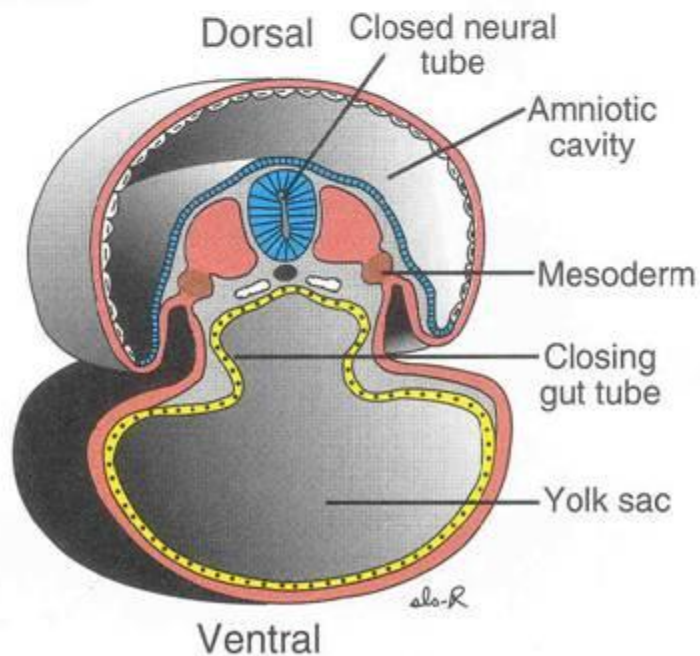




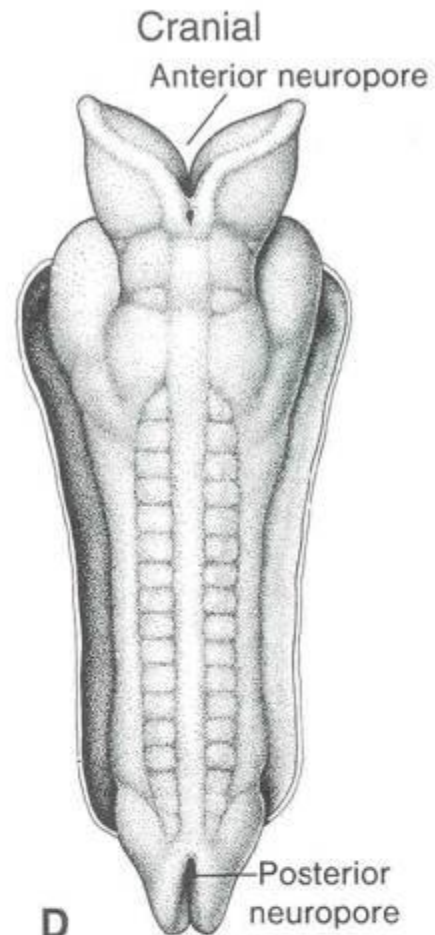
**A** Caudal  
22 Days  
Dorsal View



**B**

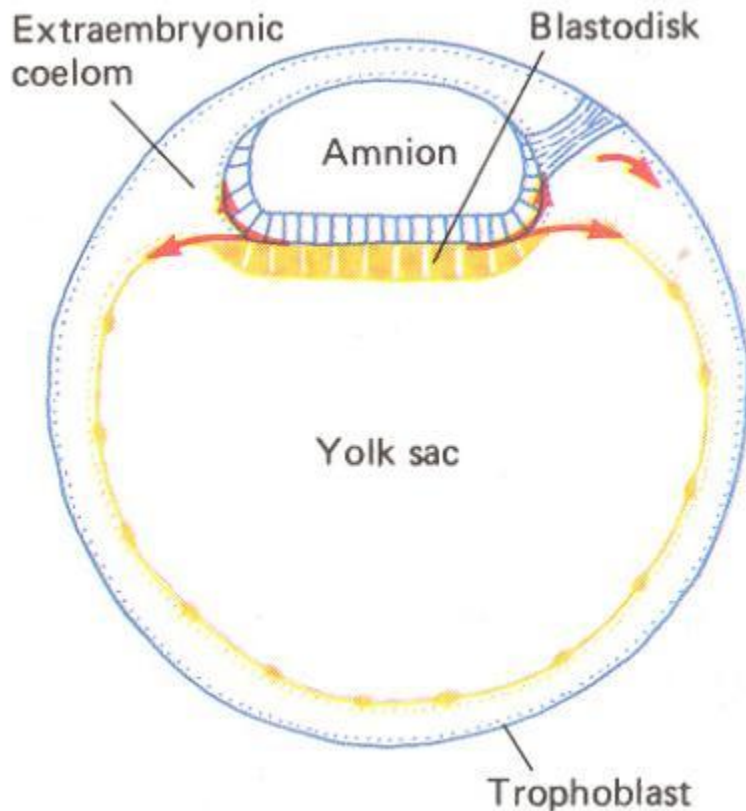


**C**



**D** 23 Days  
Dorsal View





You should note that not only has there been a relative acceleration in the precocious development of the amniotic cavity, but also in the formation of the extra-embryonic mesoderm.

In mammals, the extra-embryonic mesoderm forms in place (in situ), and does not need to get there via a long migration from the embryo proper as in reptiles and birds.

Through differential growth, the yolk sac comes to be quite small and the extra-embryonic coelom comes to be relatively enormous.

Draw here:

# TIME OUT: SOME NOTEWORTHY SIMILARITIES TO REPTILES AND BIRDS

(Recall that earlier I said that these processes are different in different mammals.)

In mammals in which the blastocyst does not become implanted in the uterus as early or as deeply (as in primates) the amnion forms more slowly, sometimes in a manner more similar to reptiles + birds.

For example in opossums, pigs, and rabbits, the inner cell mass and initial appearance of the endoderm is still in contact with the surface of the blastocyst with no cavitation to form the amniotic cavity:

At about the same time that the extra-embryonic mesoderm appears, somatopleuric amniotic FOLDS appear. Notably, they still appear before the differentiation of ectoderm and mesoderm in the prospective embryo proper.



# THE ALLANTOIS

In all mammals, an allantois appears.

As in birds and reptiles, it appears in the region that will be incorporated into the hind part of the gut and it is lined by endoderm.

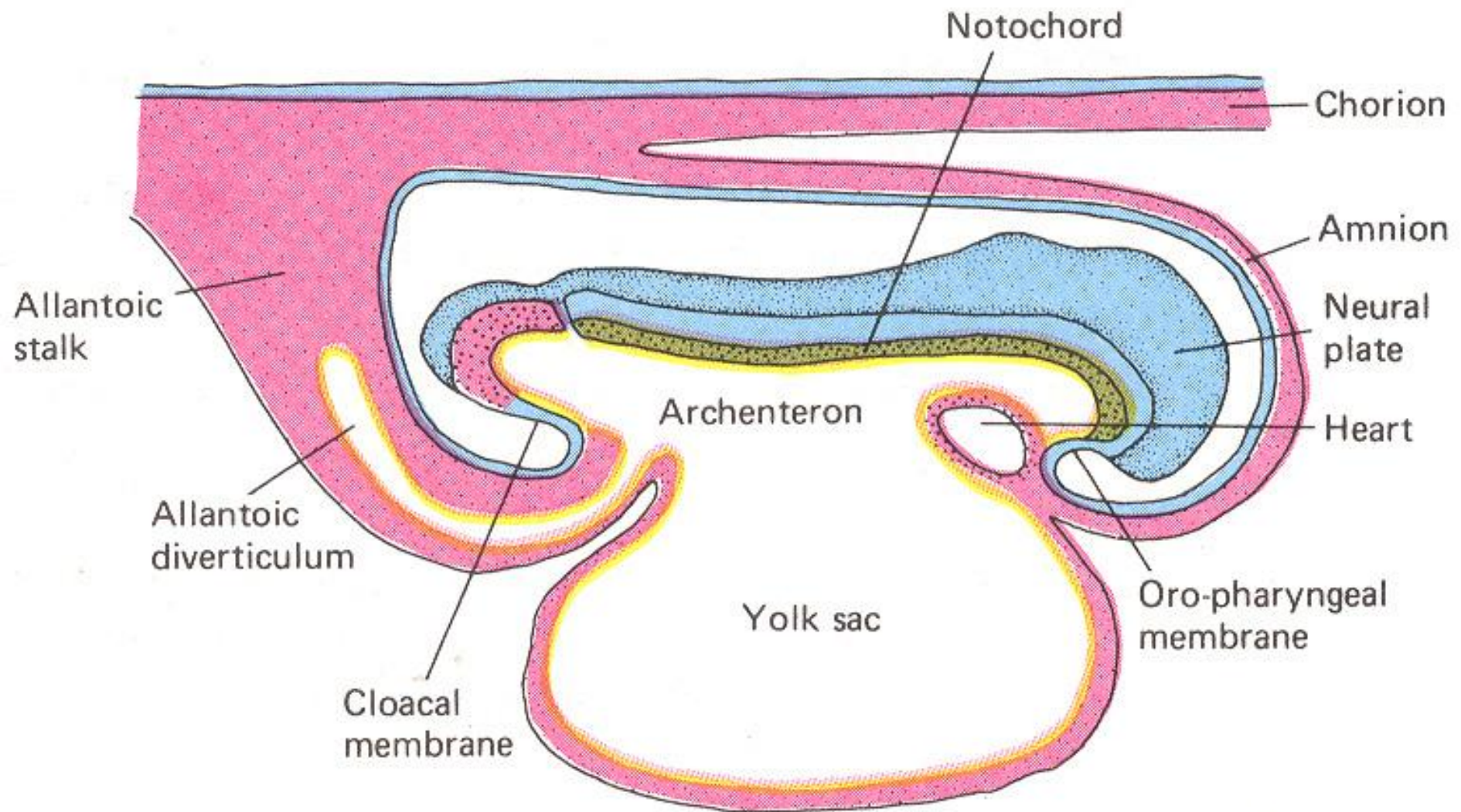
Recall that in birds it fused with the chorion to form the chorio-allantoic membrane that contacted the egg shell.

In therian mammals, there is not shell, and the exterior is the maternal uterine wall.

In the case of placental mammals, the fetal fusion of the chorion and the allantois is the **CHORIO-ALLANTOIC PLACENTA**.

A limited chorio-allantoic placenta is found in some - but not all - marsupials. Its more limited development is correlated with the fact that the gestation period is significantly less in marsupials.

In certain other marsupials (e.g. opossum, marsupial cat), there is a fascinating difference. The yolk sac expands and fuses with the chorion instead. This is called a **CHORIO-VITELLINE PLACENTA** (or a “yolk sac placenta”). This is very rarely seen in some placental mammals.



# PLACENTAL STRUCTURE

Humans and other primates are like other placentals in that the fetal placenta is chorio-allantoic. But, it is important to note that there is a wide variety of placental types.

Primates: blood vessels of the allantois carry waste and  $\text{CO}_2$  away from the embryo, and oxygen plus nourishment to it. In primates though present, the allantois is never huge as in birds. It remains relatively small, even rudimentary.

Draw here:



There are some mammals (e.g. pigs) that possess a very large allantois.

In primates, the yolk sac and allantois remain fairly small, the latter essentially reduced to an **ALLANTOIC DIVERTICULUM**.

The mesoderm and ectoderm of the chorion form villi that make for a close contact between the fetal and maternal parts of the placenta.

As the amniotic cavity continues to expand and obliterate the extra-embryonic coelom, it comes to surround the embryo entirely except at the body stalk.

The rudimentary allantois in humans lies within the body stalk and the yolk sac comes to be imbedded in it as well.

It is the body stalk that carries the allantoic blood vessels and is therefore, the body stalk that gives rise to the umbilical cord.

Different groups of mammals show a great variety of patterns of chorionic coverage contributing to the fetal placenta. In humans and other primates, it is disc shaped, and thus referred to as discoidal.

## PLACENTA TYPES:

- DISCOIDAL - humans and other primates, bears
- DIFFUSE - e.g. pigs
- ZONARY - dogs
- COTYLEDONARY - sheep.

# THE PRIMITIVE PLACENTAL CONDITION

Presumably, the primitive type of placenta is a condition where the endothelial walls, blood vessels, and mucosa of both the mother and the fetus remain intact. This is known as an **EPITHELIOCHORIAL PLACENTA**.

- **SYNDESMOCHORIAL** - when maternal epithelium is broken down (e.g. cows).
- **ENDOTHELIOCHORIAL** - when maternal epithelium ***and*** mucosa are both broken down (e.g. dogs).
- **HEMOCHORIAL** - when ***all*** of the maternal tissues are broken down to the point that the fetal epithelium is literally bathed directly by the maternal blood cells (e.g. humans, other primates, rodents)
- (Essentially, all this has to do with the degree of destruction of the maternal part of the placenta.)

The closer the relationship between the fetal and maternal portions of the placenta, the closer the physical connection.

Where there is a very close union, there is loss of maternal tissues at birth, and the placenta (as in humans) is said to be **DECIDUOUS**. Other types of placentae show intermediate conditions.

# SUMMARY: EMBRYONIC DEVELOPMENT SEQUENCE



# Structures Visible in the Basic Cross-Section of the Body (Embryo or Adult!)

- Coelom
- Somatopleure
- Splanchnopleure
- Parietal Peritoneum
- Visceral Peritoneum
- Dorsal mesentery
- Ventral mesentery

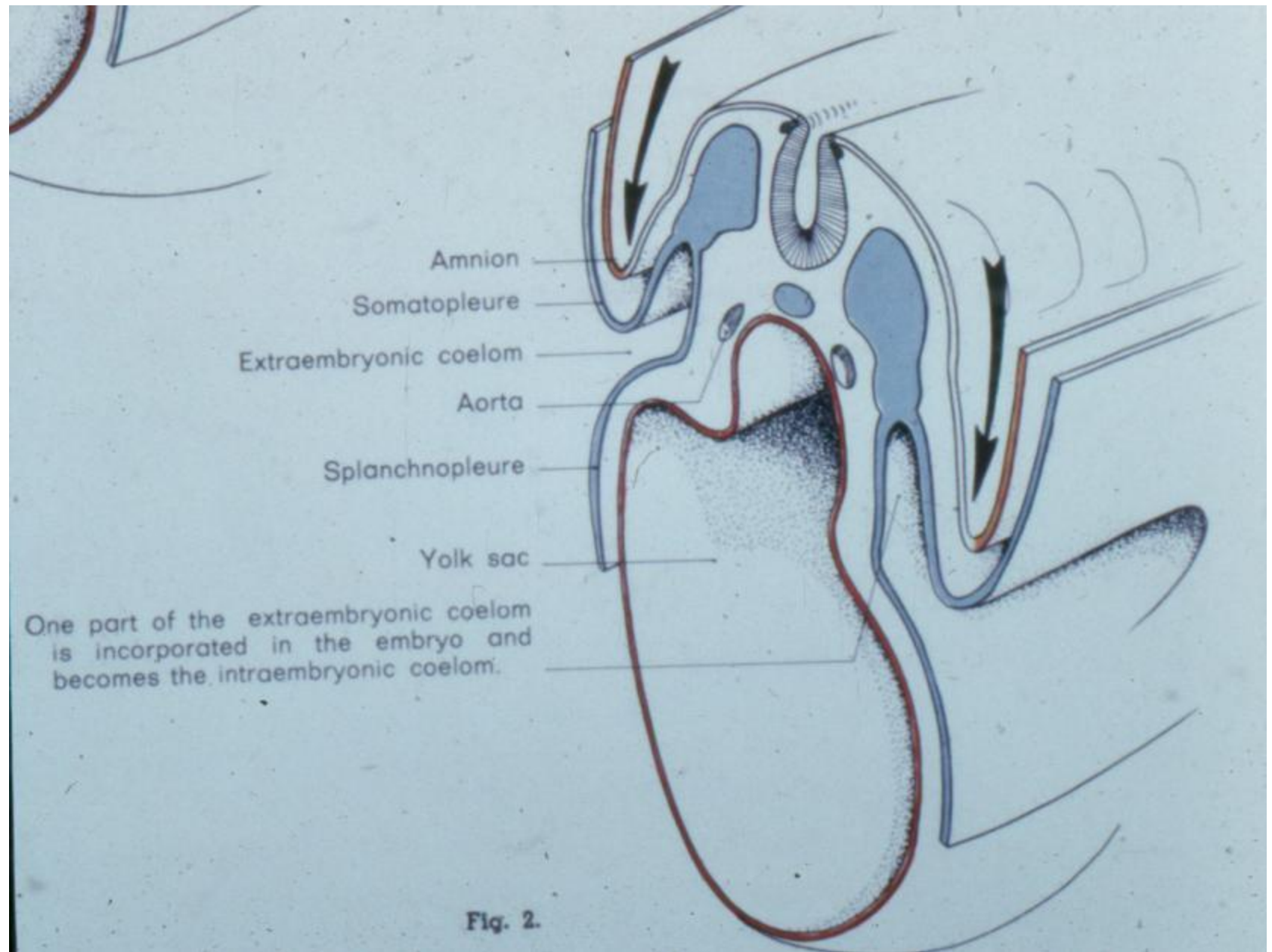
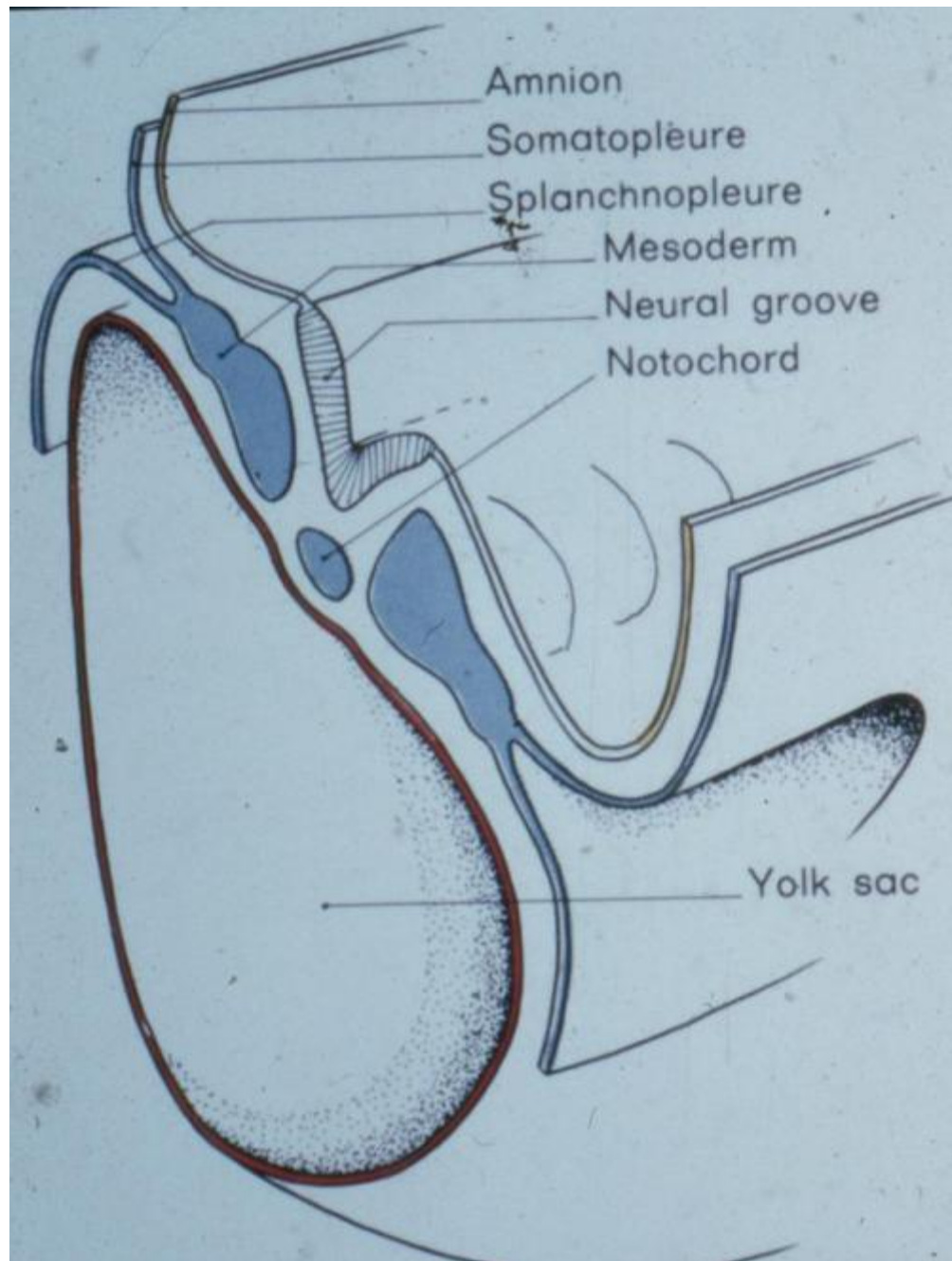


Fig. 2.



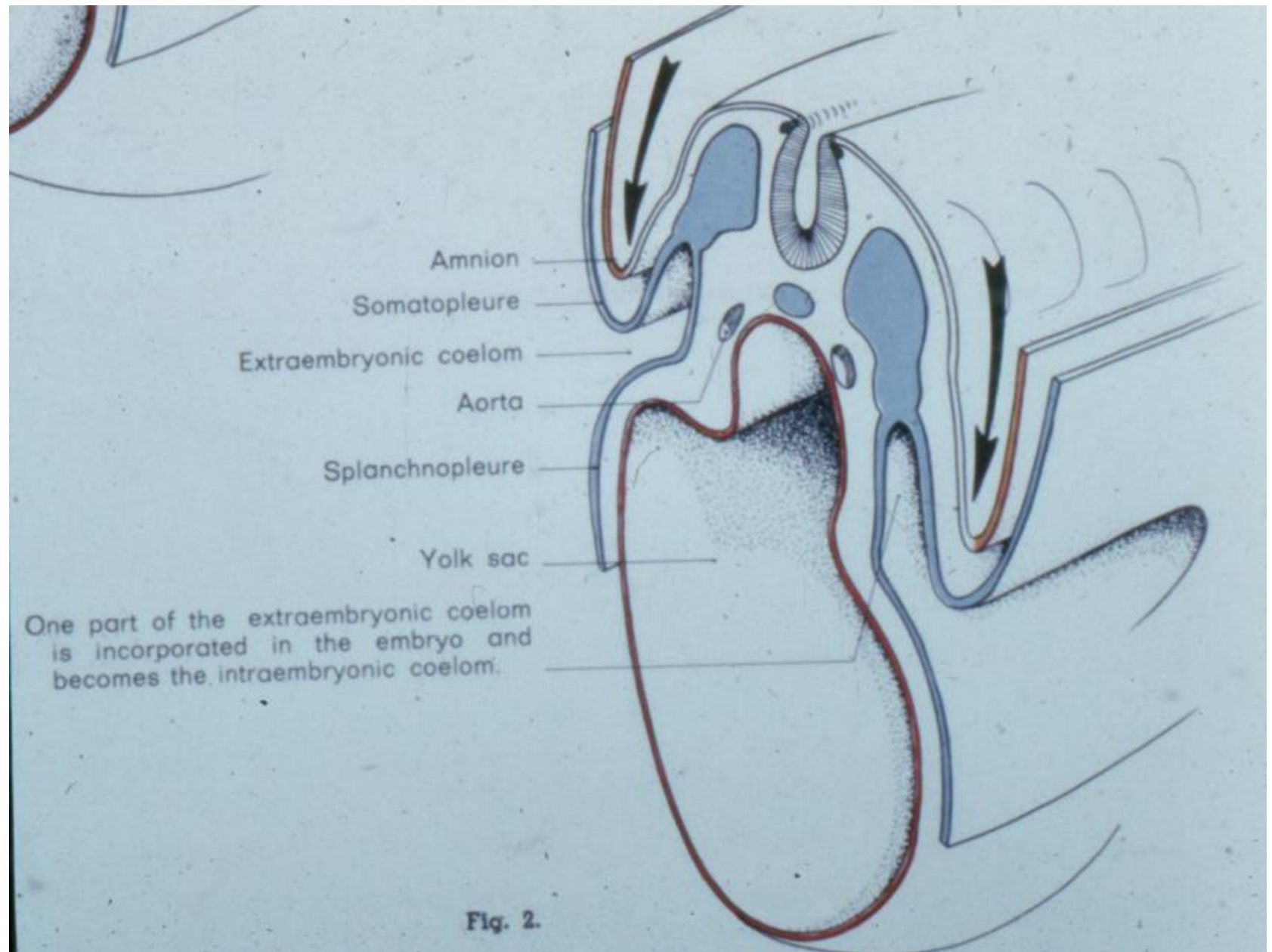
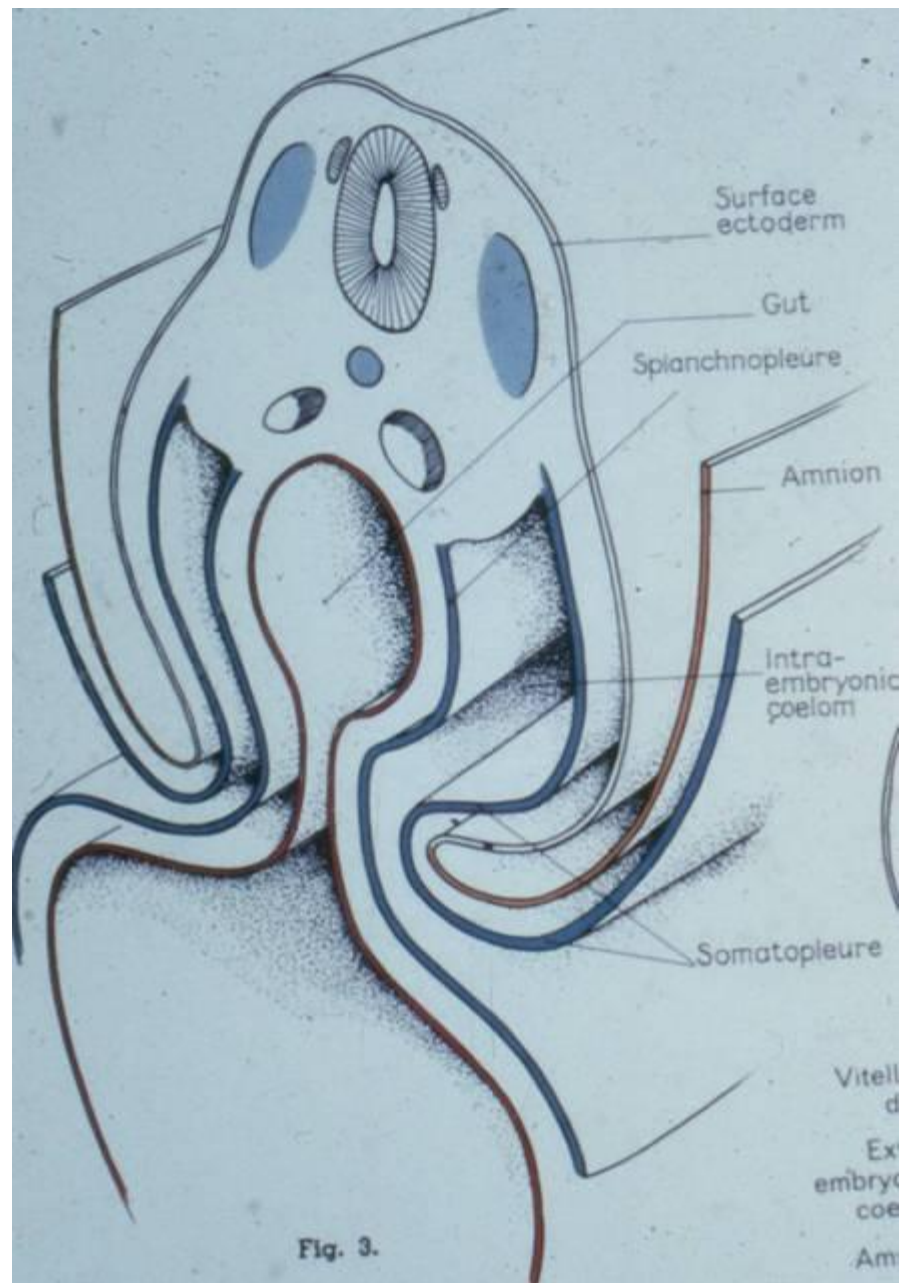
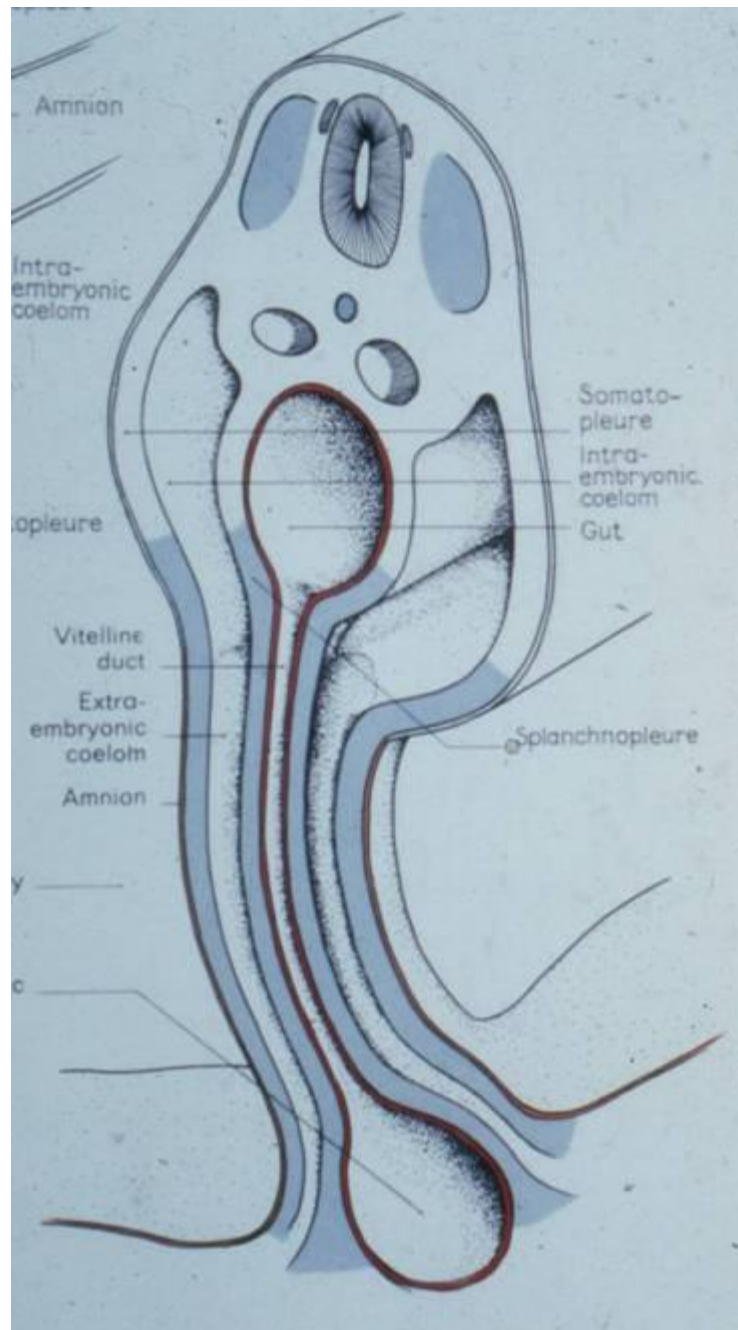


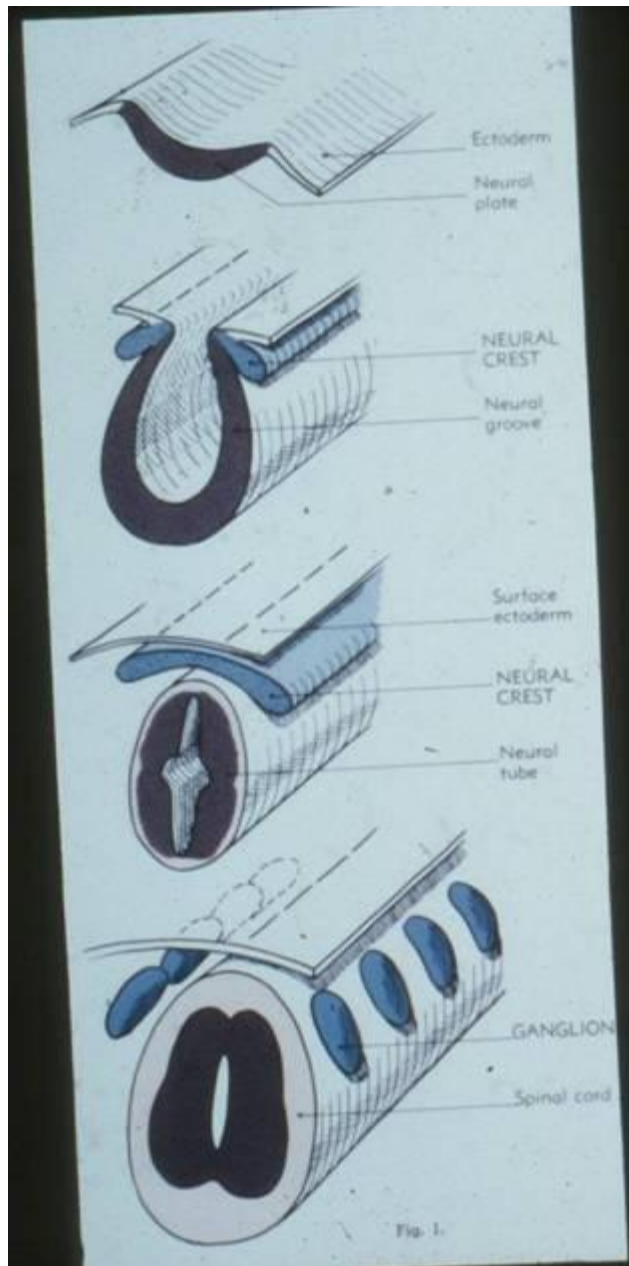
Fig. 2.

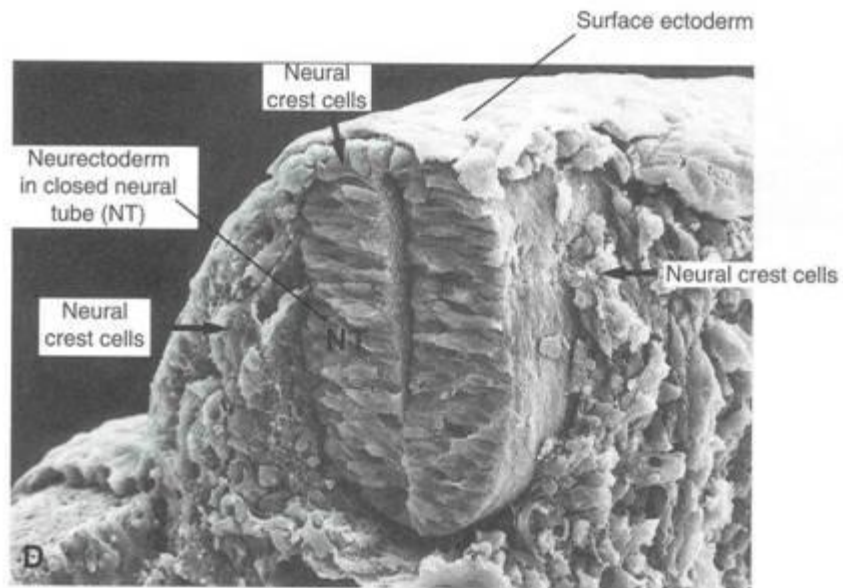
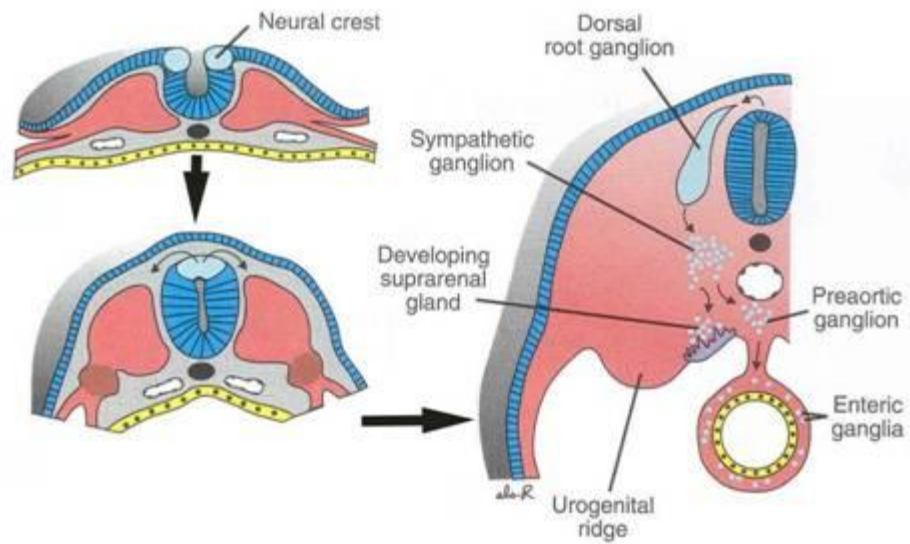




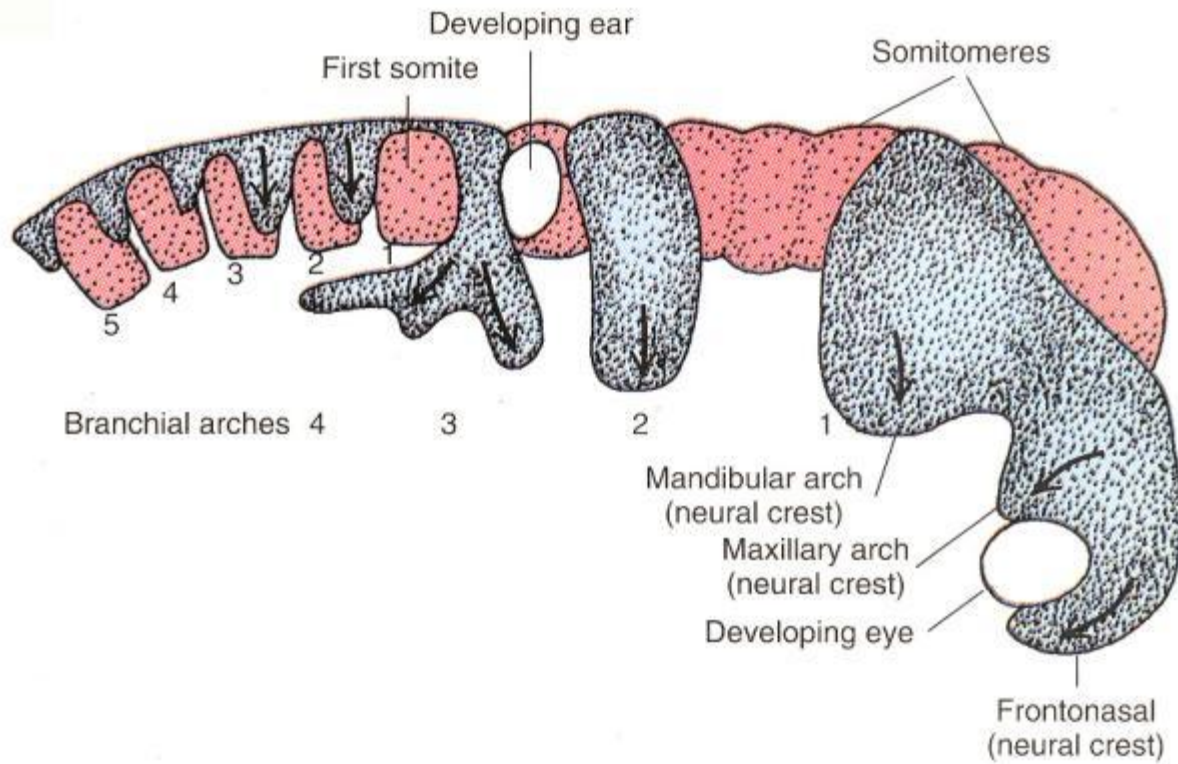
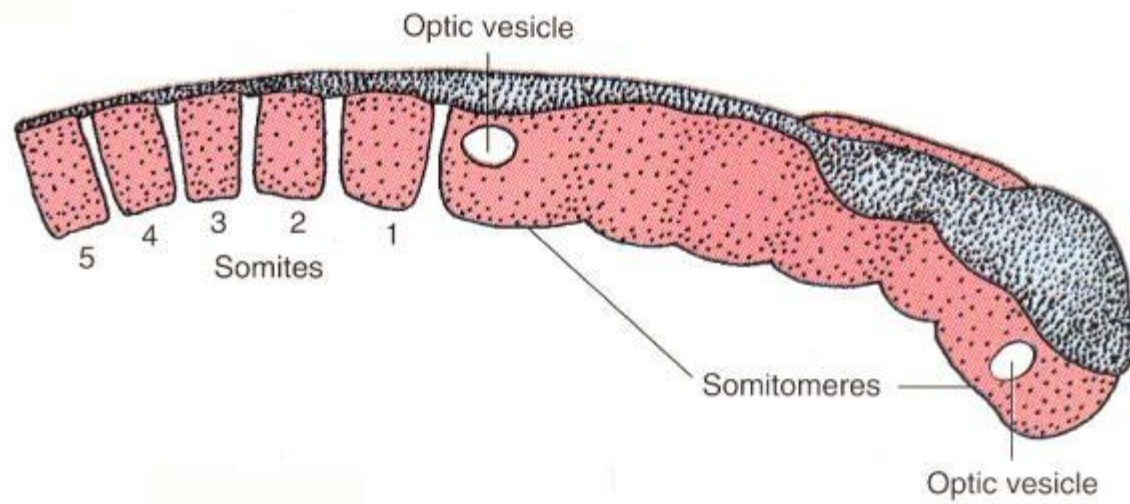


# Neural Crest Development

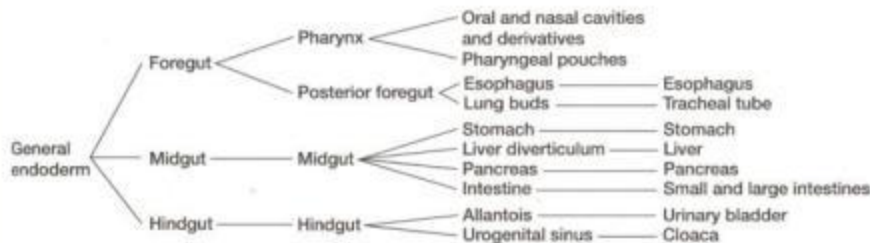
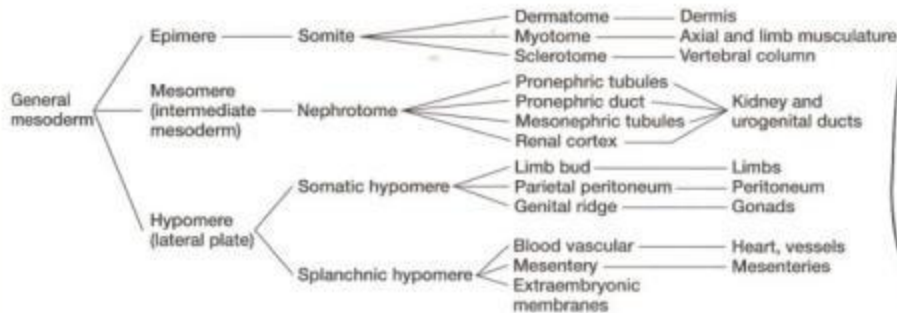
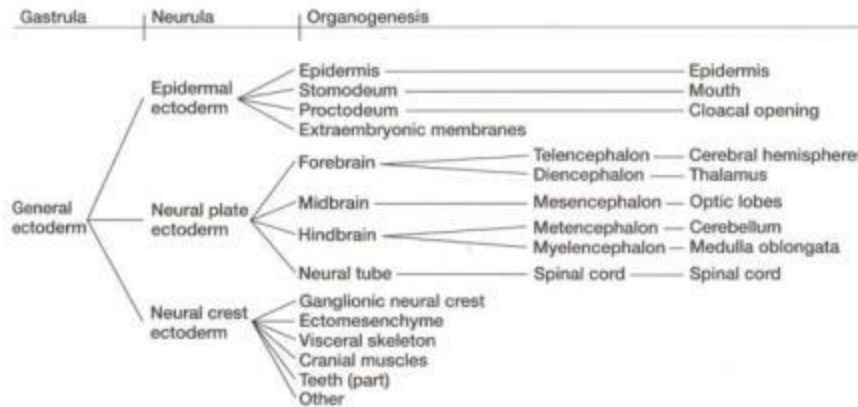




23 Days

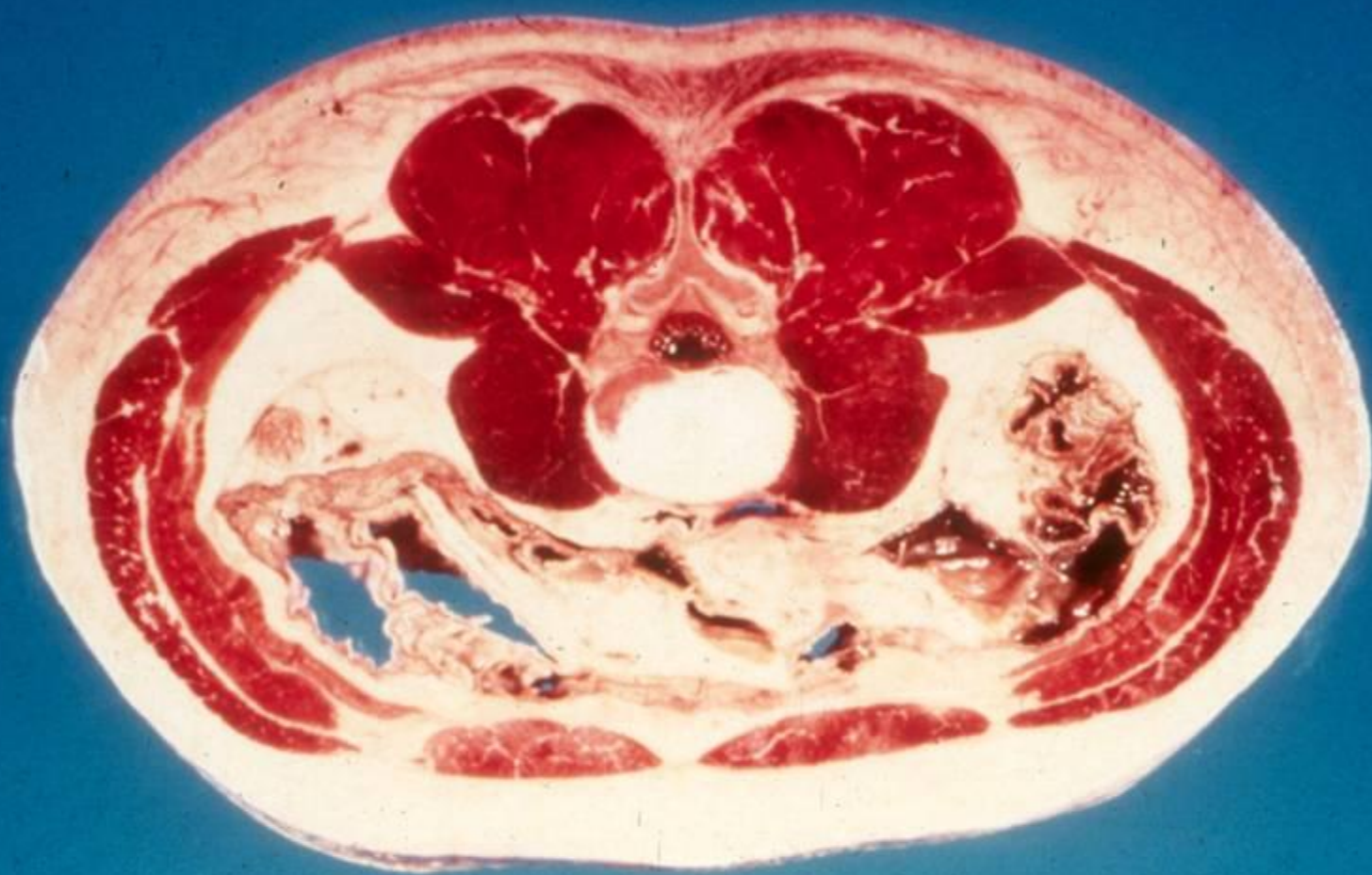




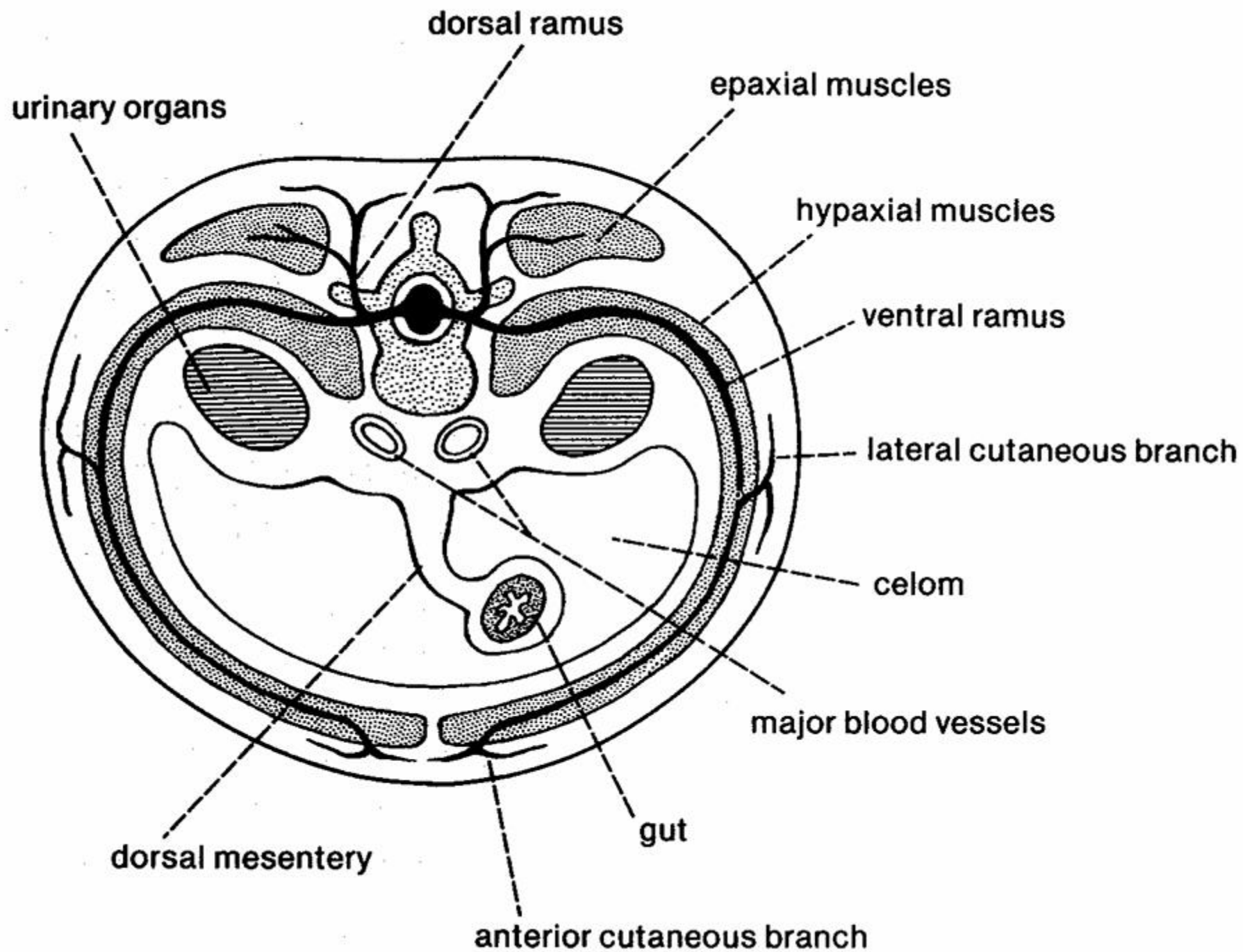




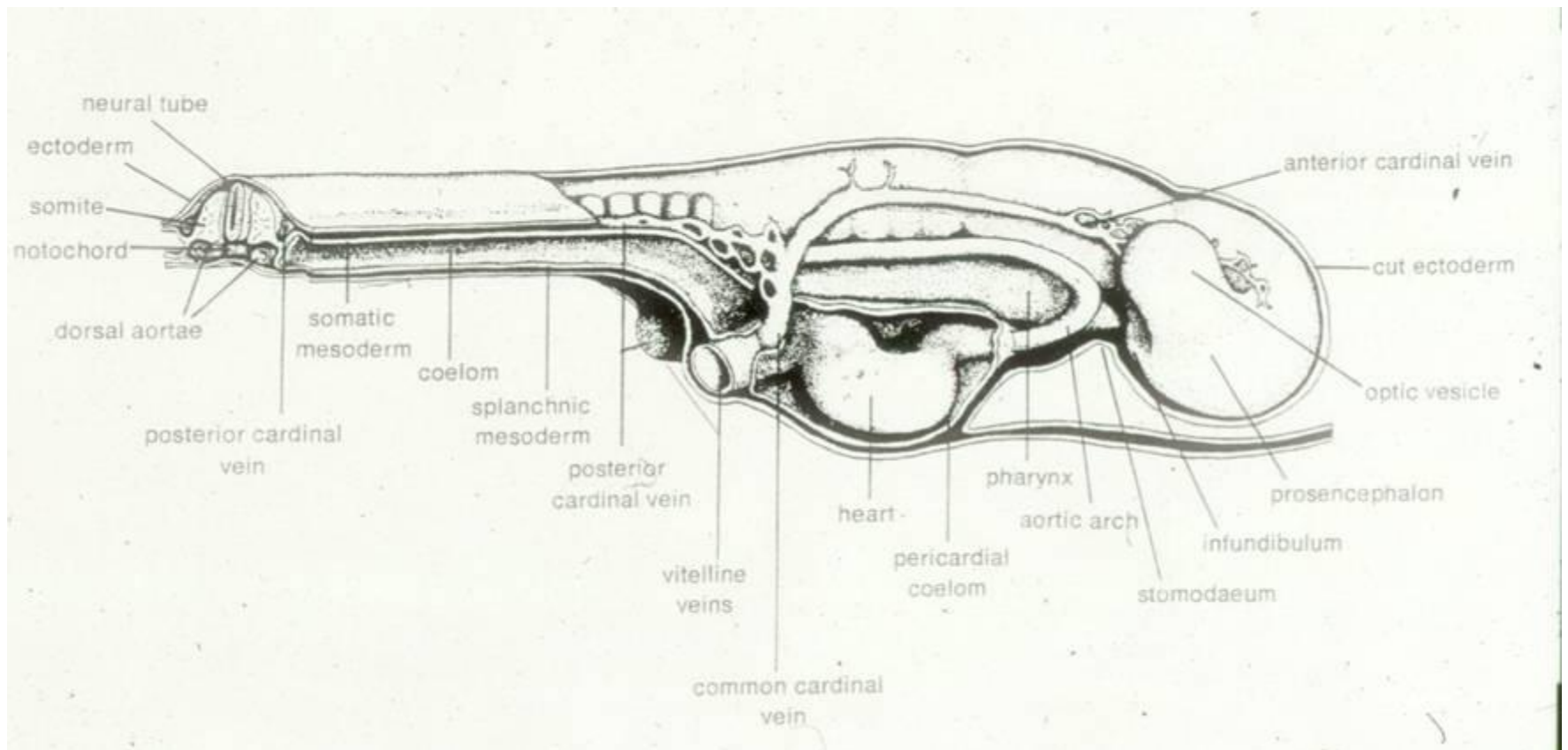
Test yourself...



7



# Trans-segmental structures versus Segmental structures



28-DAY-OLD EMBRYO. CHORION AND AMNION REMOVED.  
SIDE OF RED SQUARE = 1/16 INCH.



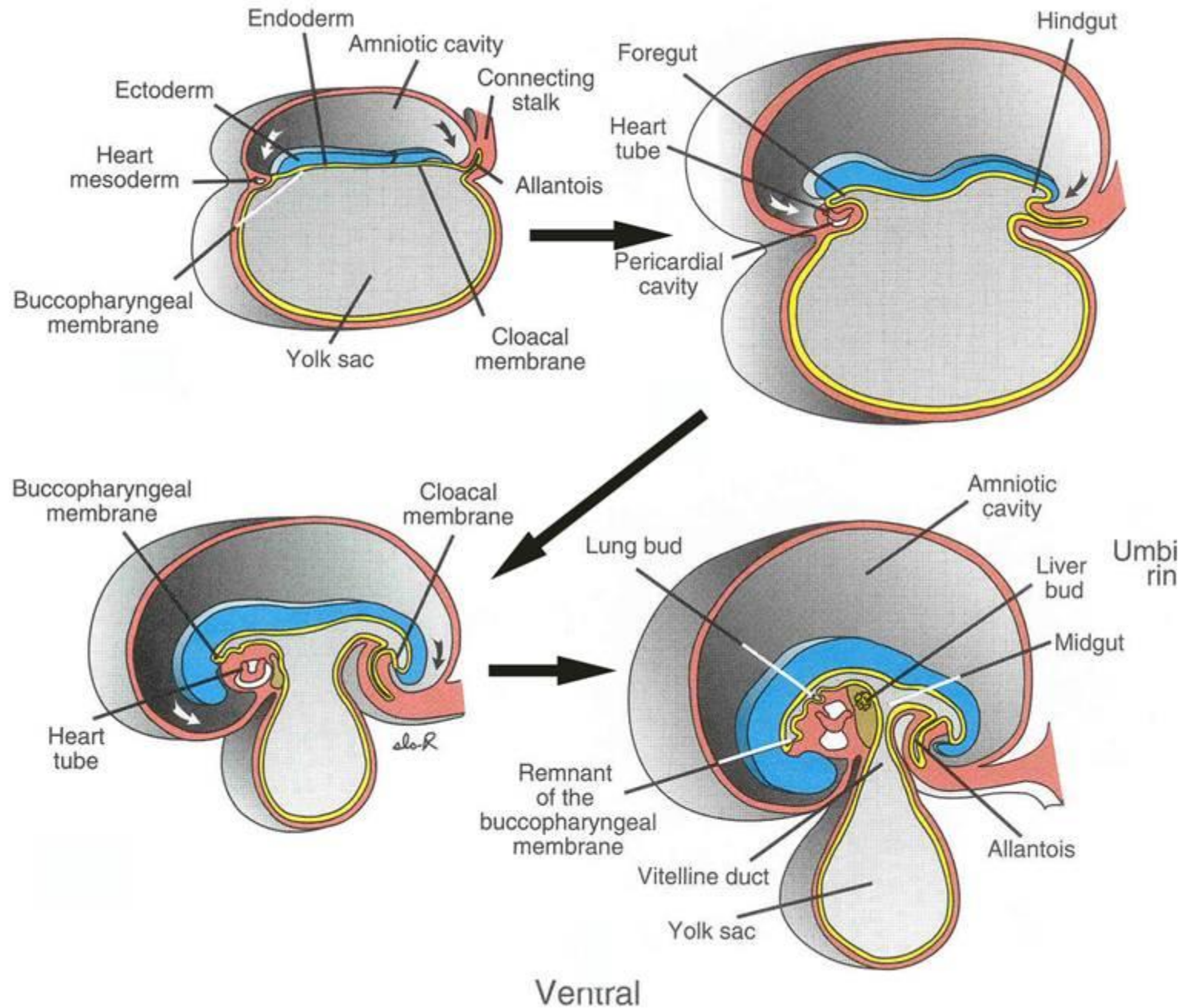
Gill slits / Gill pouches



# Further endodermal development:

- Lateral folds
- Oropharyngeal membrane
- Embryonic foregut
- Embryonic hindgut

Dorsal



# FUNCTIONAL AND PHYLOGENETIC SUMMARY

The comparative study of chordate ontogenies is, to a great extent, a study of the amount of yolk and the origin of extra-embryonic membranes.

Extra-embryonic membranes are not extraneous materials. They serve the developing embryo and figured significantly in the evolution of the fully terrestrial Amniota.

Map the important features onto a phylogeny:

# 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.

Urochordata

Cephalochordata

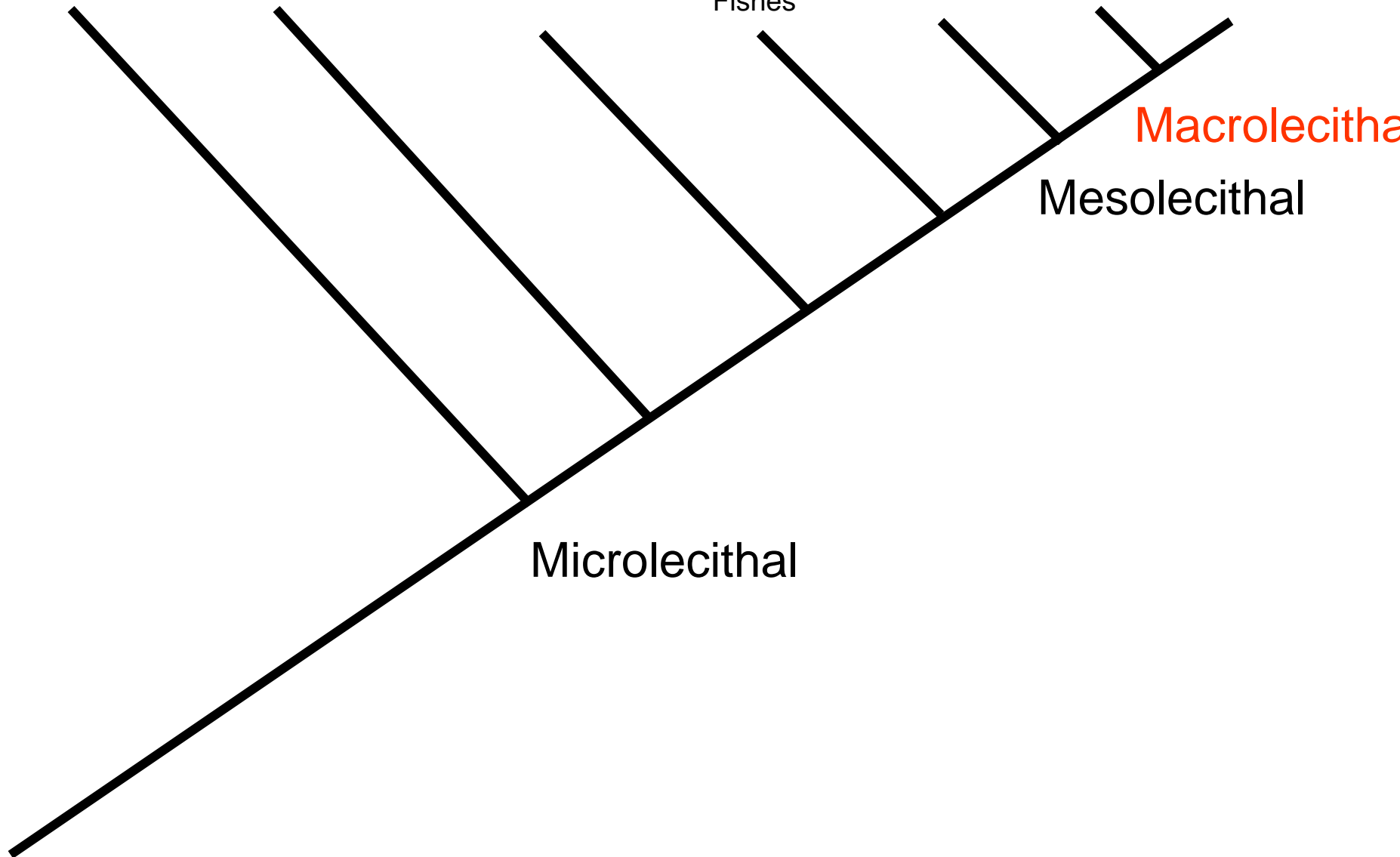
Jawless Fishes

Gnathostome  
Fishes

Amphibia

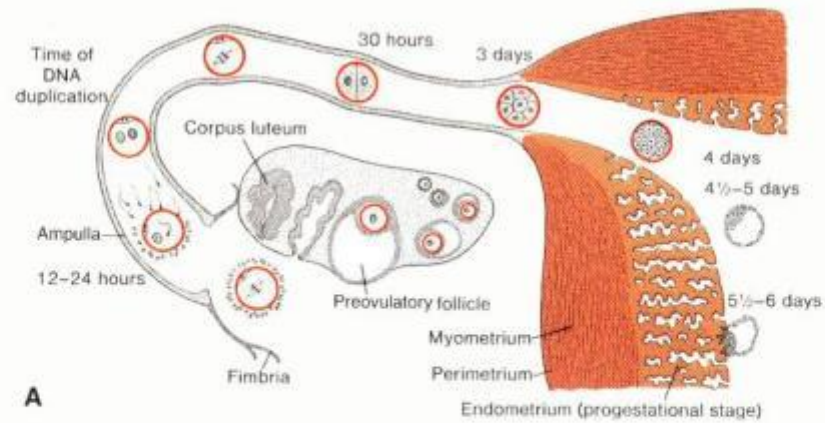
Synapsida

Reptilia

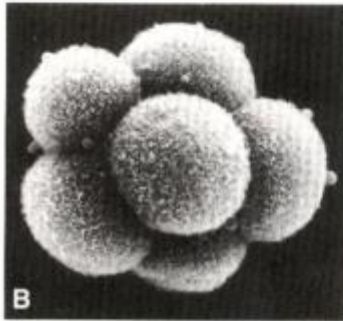


# SUMMARY: EMBRYONIC DEVELOPMENT SEQUENCE

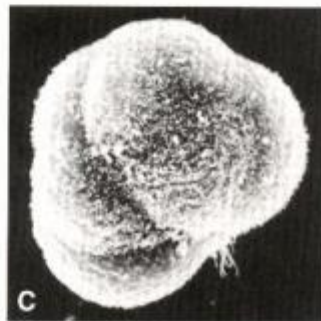




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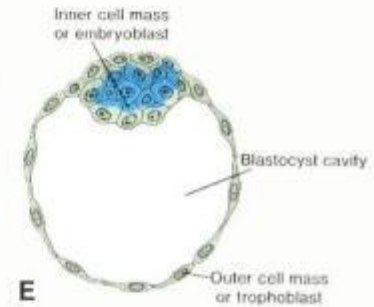
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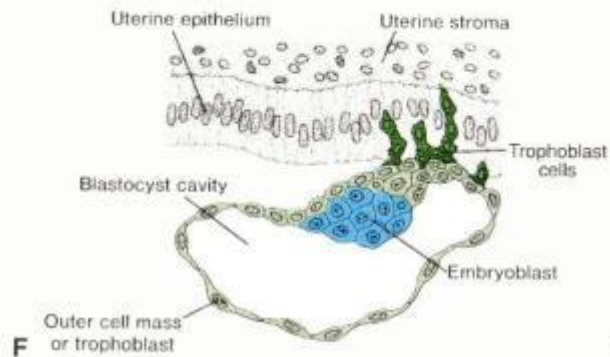
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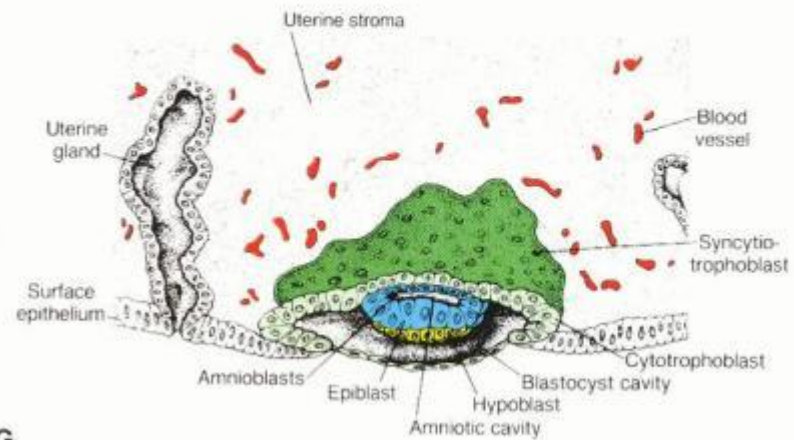
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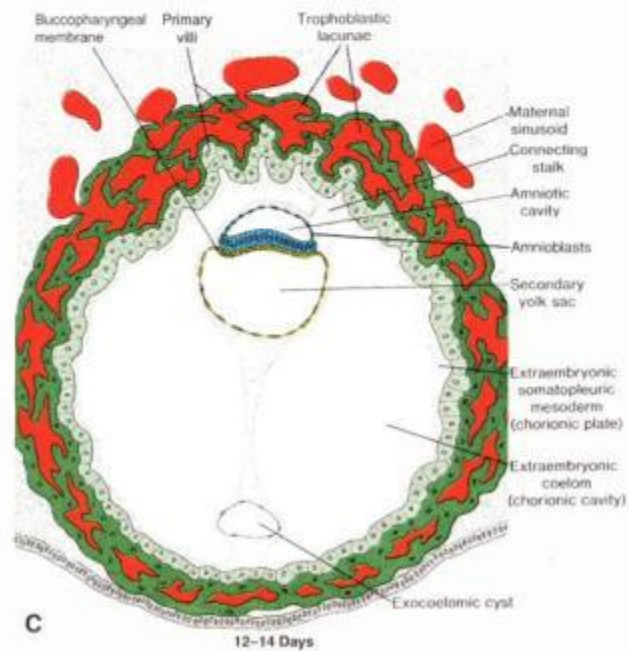
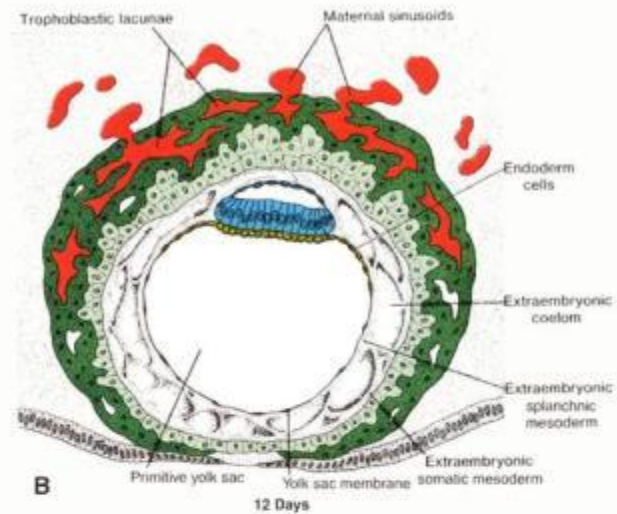
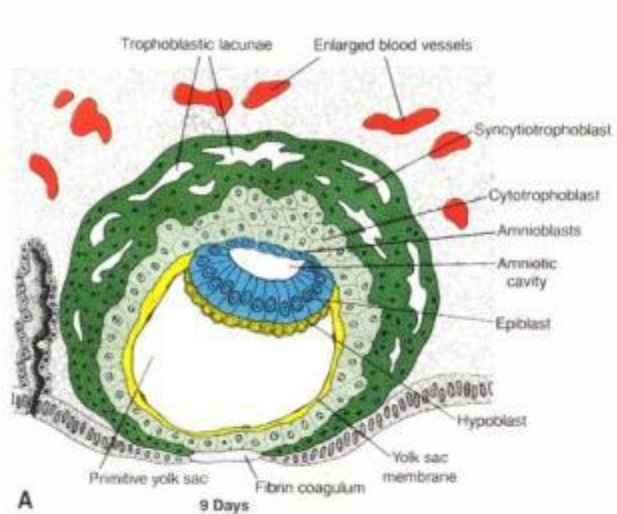
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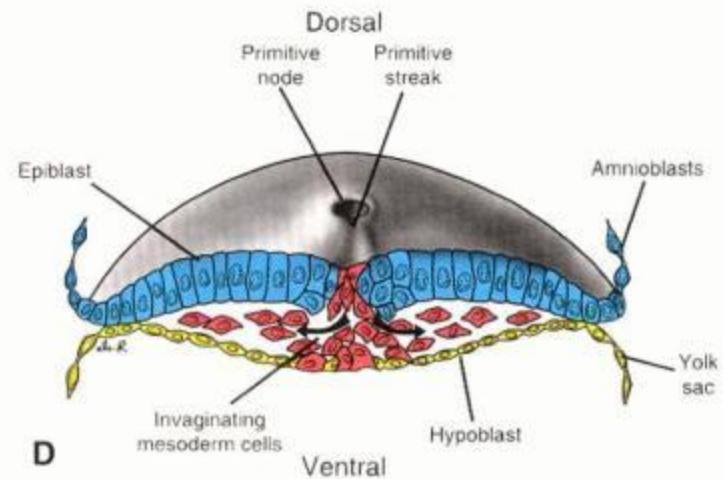
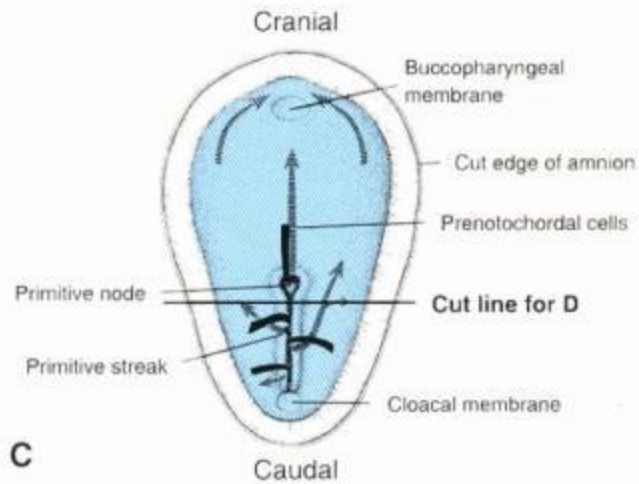
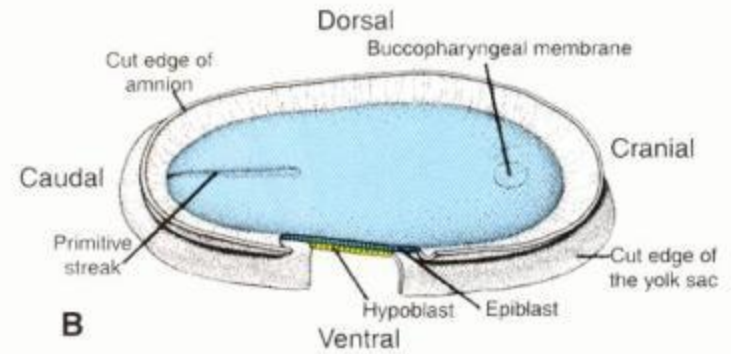
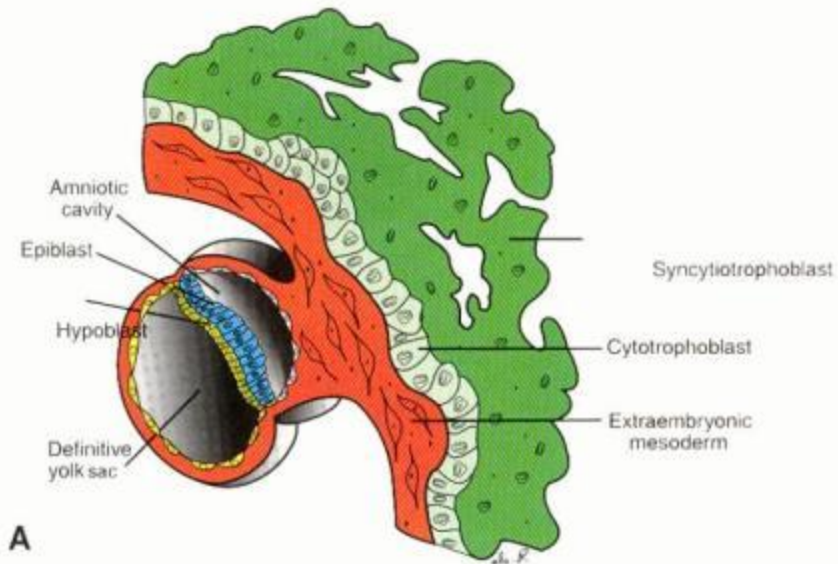


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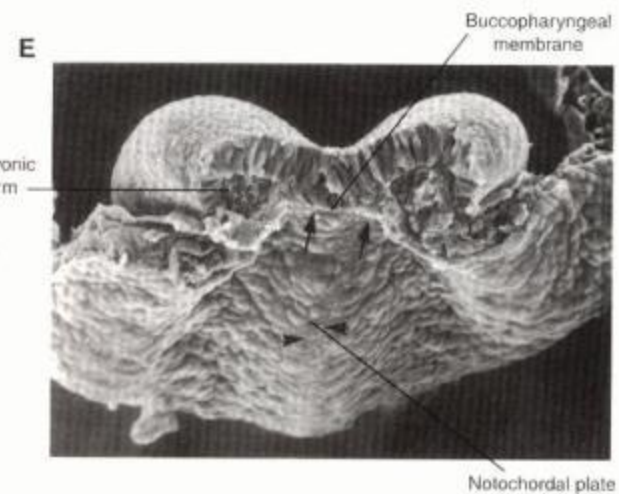
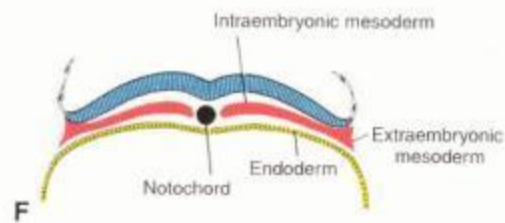
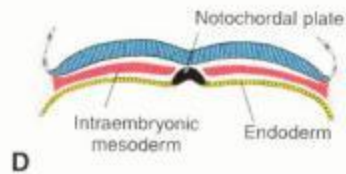
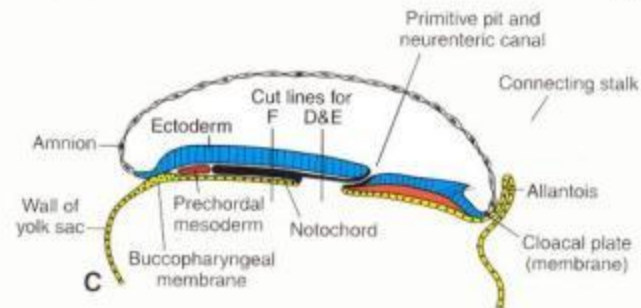
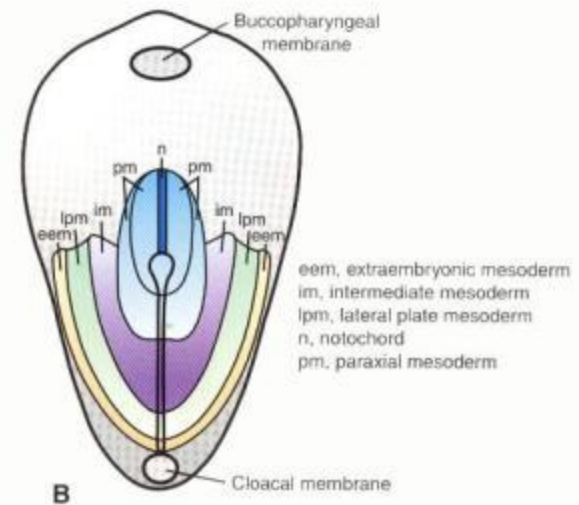
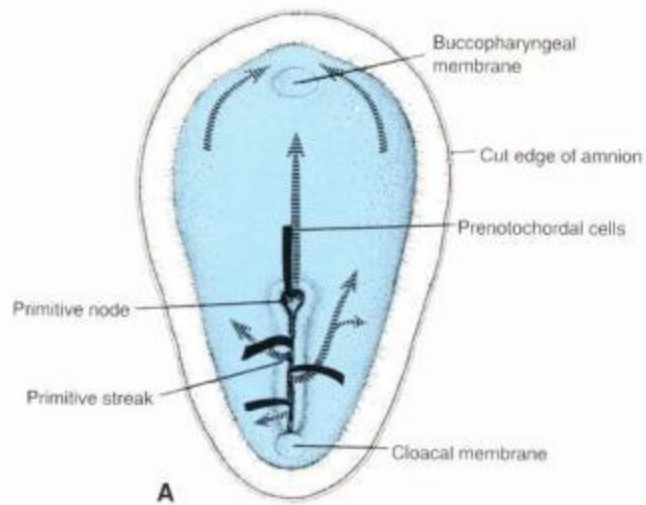


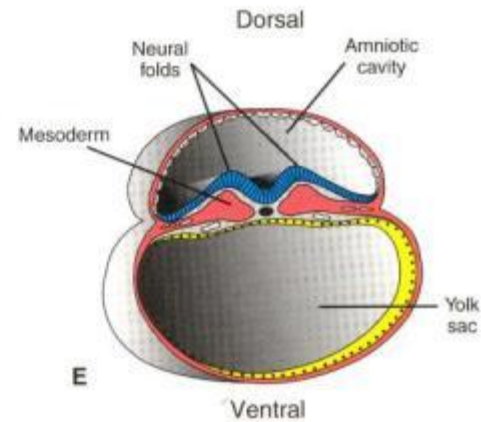
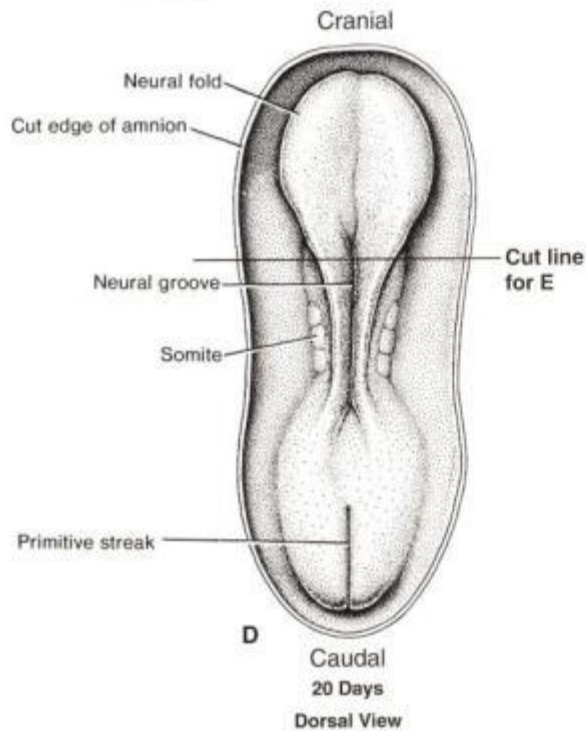
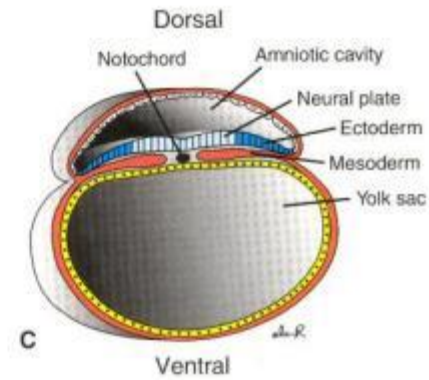
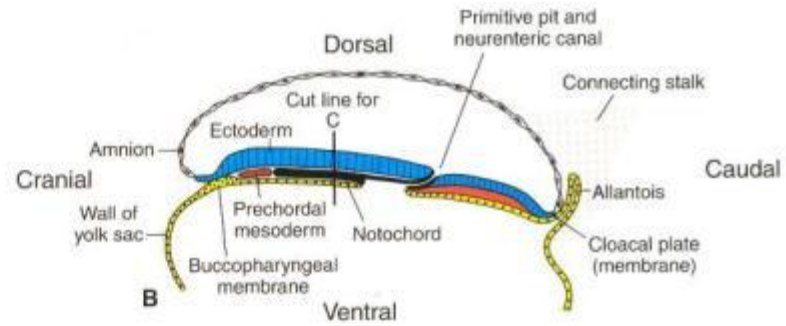
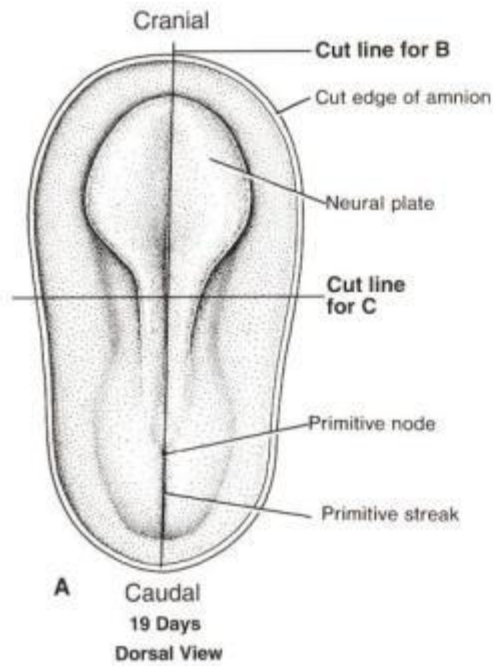
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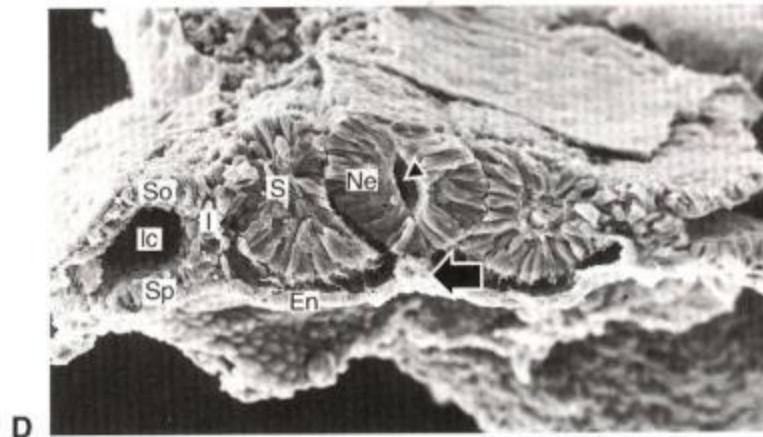
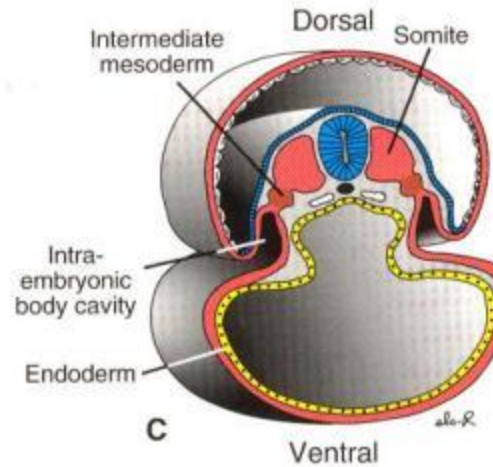
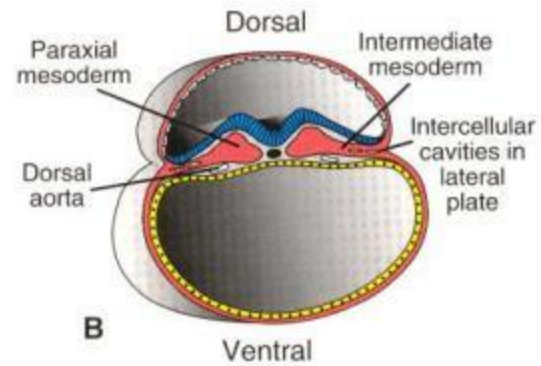
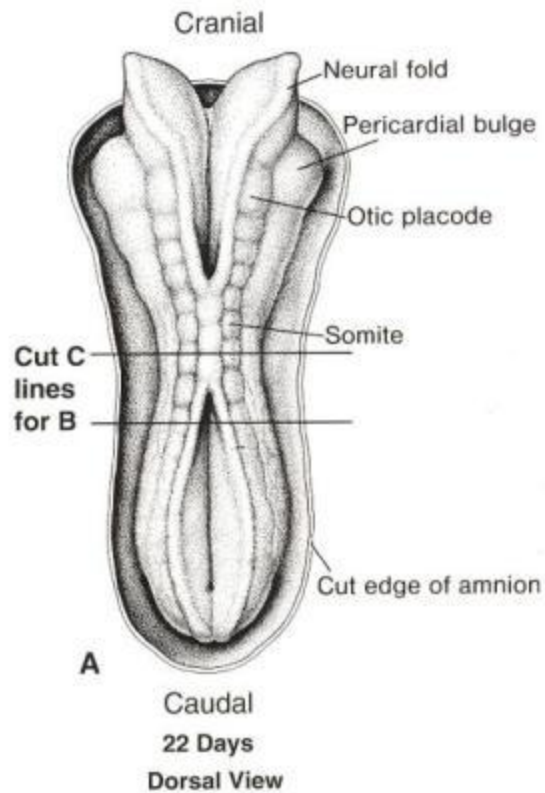






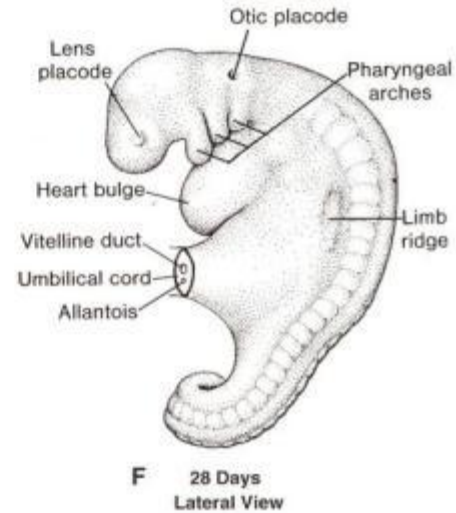
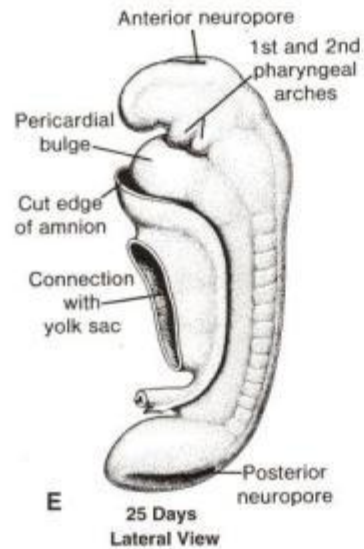
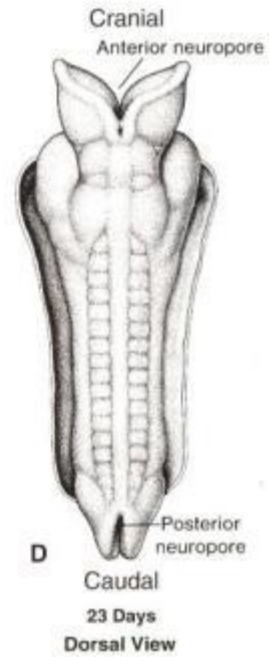
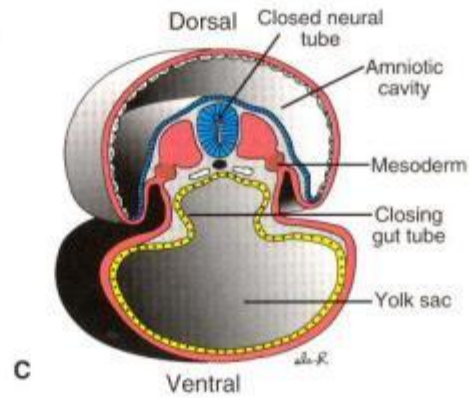
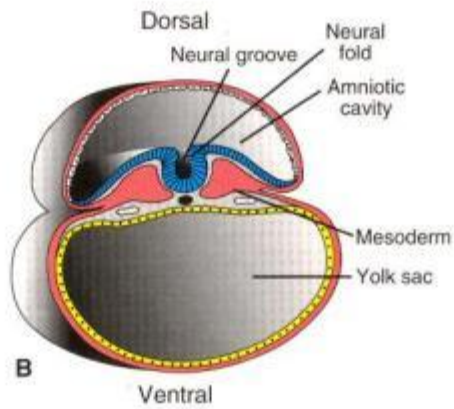
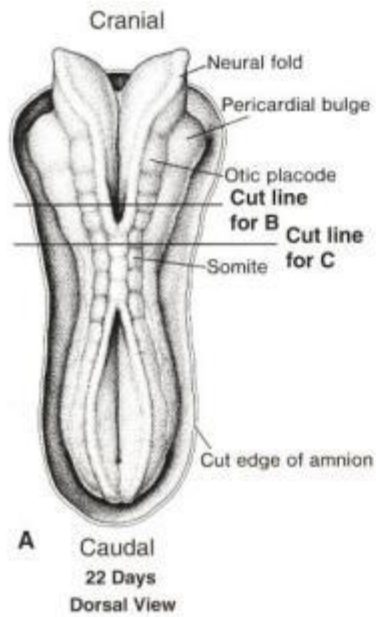


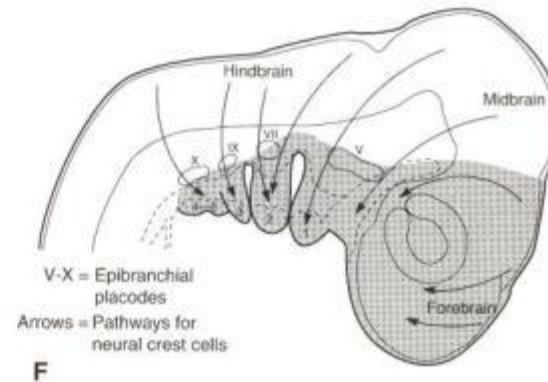
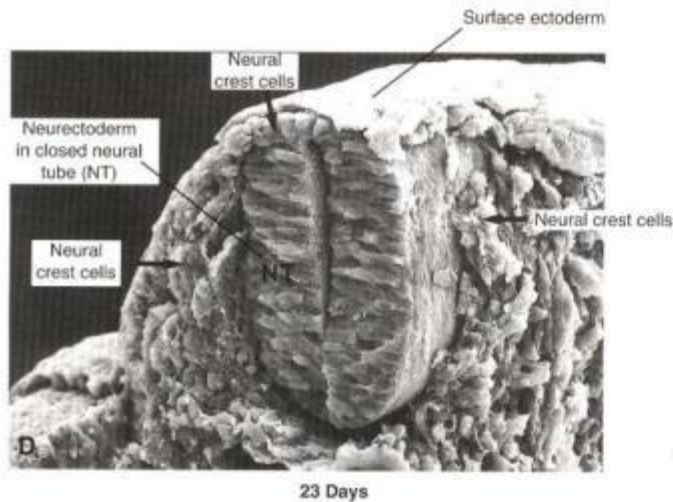
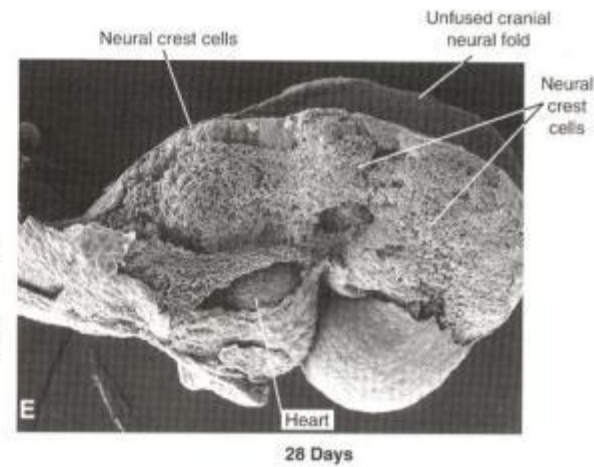
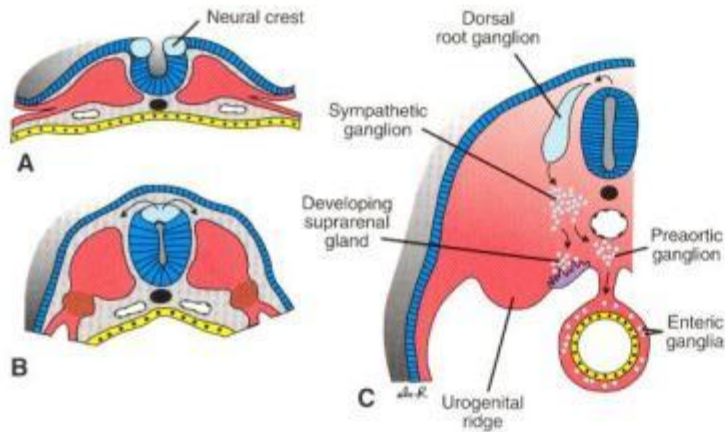




En, endoderm  
I, intermediate mesoderm  
Ic, intraembryonic cavity  
Ne, neural tube  
So, somatic layer  
Sp, splanchnic layer  
arrowhead, neural lumen  
arrow, notochord







**Table 3.1. Neural Crest Cell Derivatives**

- Connective tissue and bones of the face and skull
- Cranial nerve ganglia
- C cells of the thyroid gland
- Conotruncal septum in the heart
- Odontoblasts
- Dermis in the face and neck
- Spinal (dorsal root) ganglia
- Sympathetic chain and preaortic ganglia
- Parasympathetic ganglia of the gastrointestinal tract
- Adrenal medulla
- Schwann cells
- Glial cells
- Arachnoid and pia-mater (leptomeninges)
- Melanocytes

