

Biology 340

Comparative Embryology

Lecture 4

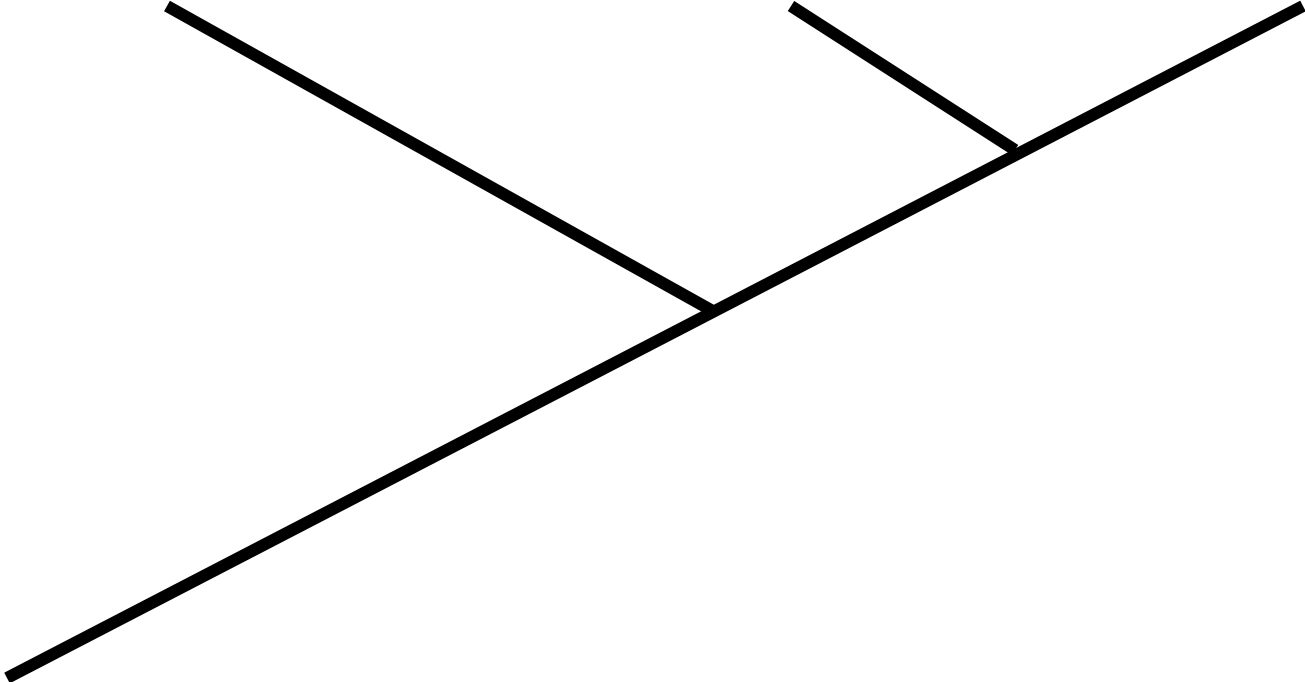
Dr. Stuart Sumida

Overview of Pre-Metazoan and Protostome Development (Insects)

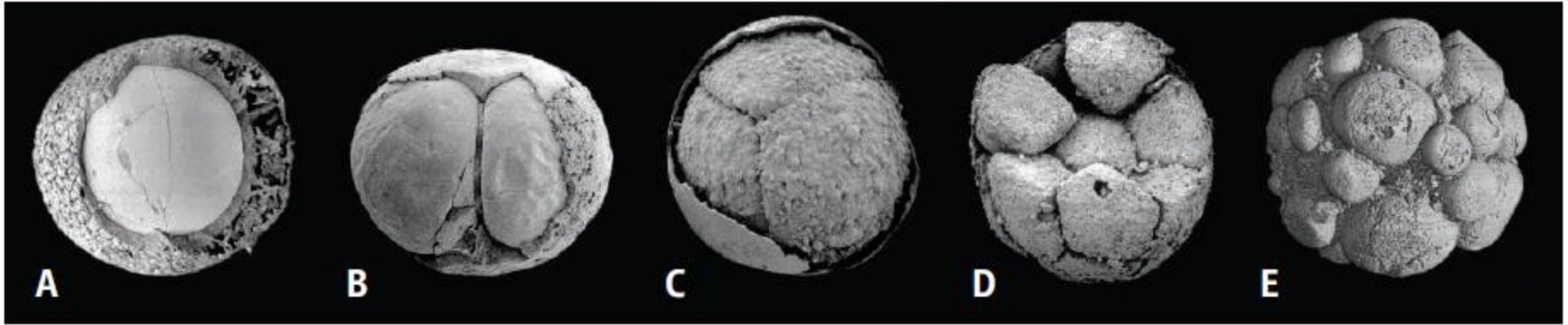
Plants

Fungi

Animals



Doushantuo "embryo" fossils



In 1998 fossilized animal embryos were reported from the early Ediacaran age Doushantuo Formation of South China (approximately 600 million + years old).

The Doushantuo fossils were interpreted as animals based largely on the recognition of a developmental pattern involving serial cell division without accompanying size increase, a process known as **palintomy**.

Many workers worried about the absence of a differentiated outer layer of cells (epithelium) on later-stage embryos, one of the hallmarks of extant (currently living) animals.

The fossils might be alternatively interpreted as “stem-group” metazoans, yet to acquire the full suite of characters expected in the last common ancestor of living forms.

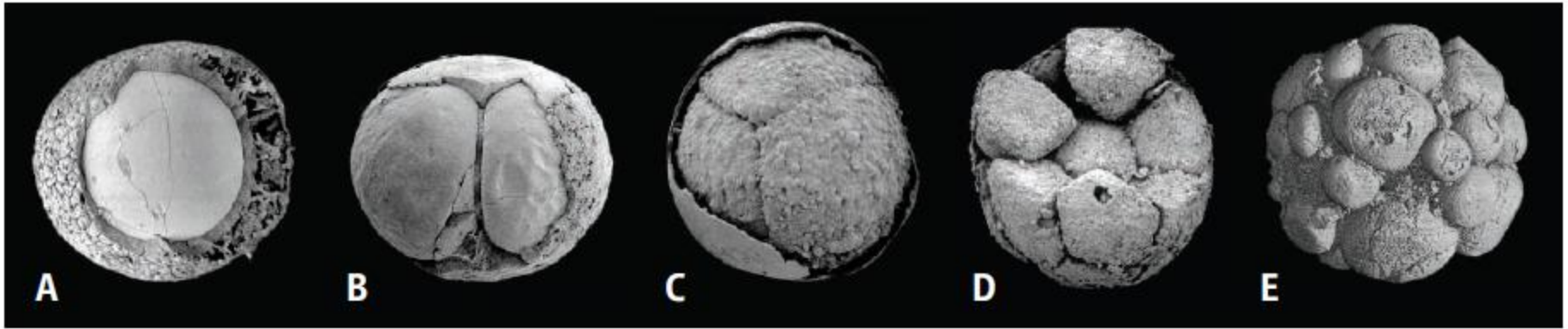
Then in 2007 came a report documenting the same size and arrangement of cells in the modern sulfur-oxidizing (and phosphate-concentrating) bacterium known as *Thiomarginata*.

It turns out they do have eukaryotic nuclei. However, they have an ontogenetic trajectory entirely foreign to the Metazoa.

Instead of developing a differentiated epithelium, the constituent cells simply continue to divide palintomically, giving rise to thousands of tiny cells

Although unquestionably eukaryotic, the fossils are not metazoan, or even properly multicellular by all appearances. They may be more like colonial *Volvox* accumulations.

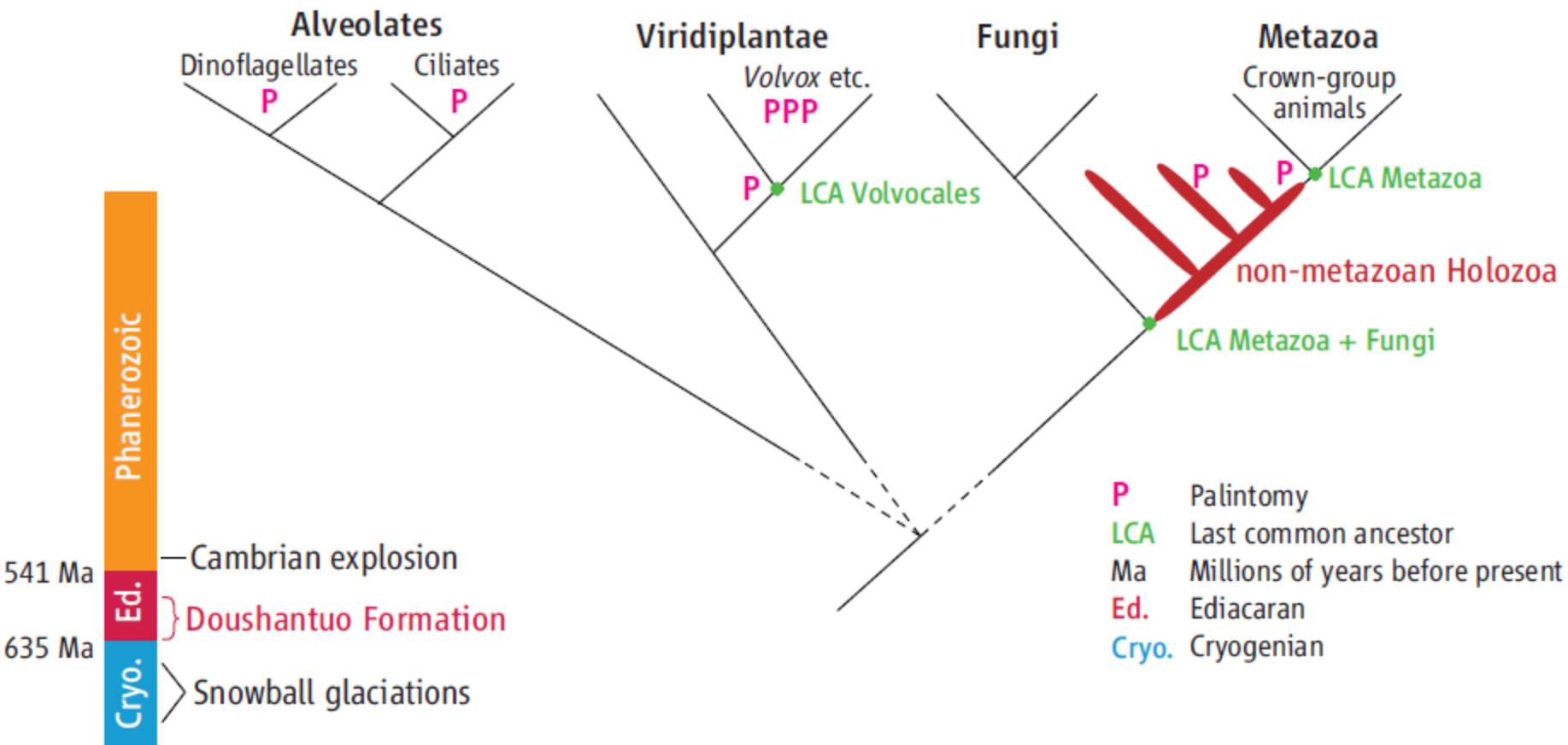
Doushantuo "embryo" fossils



Volvox carteri f. *nagariensis*



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So what exactly are they?

They have a similar style of palintomic division and overall deformation exhibited by certain kinds of “nonmetazoan holozoans,” (a mixed bag of mostly unicellular eukaryotes that evolved after the last common ancestor of animals and fungi, but before the last common ancestor of living animals).

Regardless, it is clear that palintomy evolved in the lineage leading to animals very early long before what we properly call metazoans, let alone bilateralians.

PHYLOGENETIC CONTEXT:

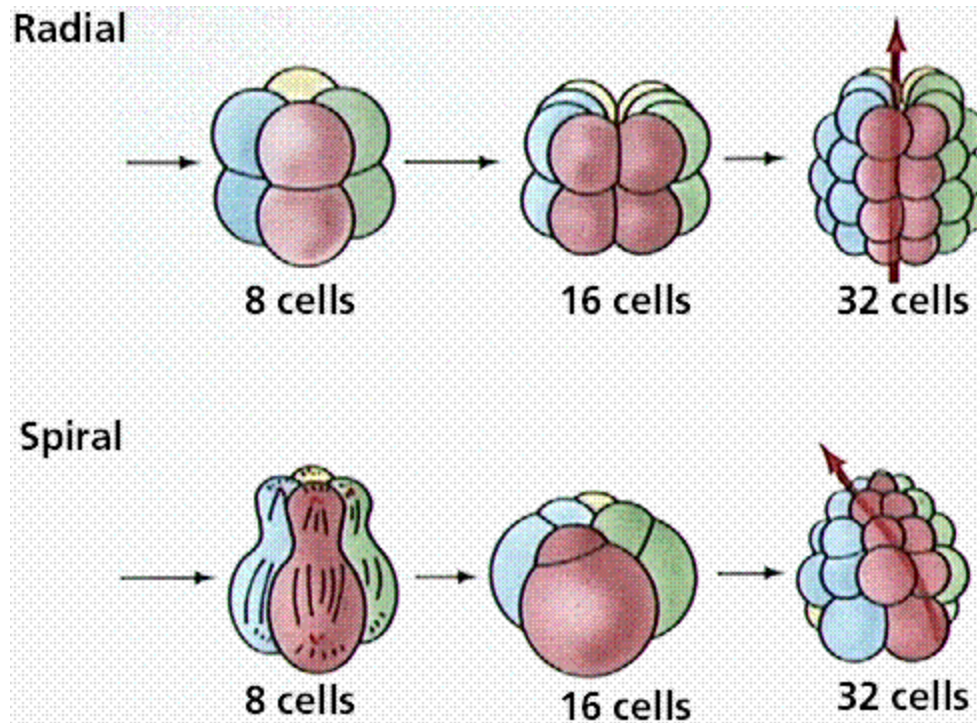
Recall that Bilateria includes two great groups of organisms – Protostomia and Deuterostomia, each of which has a bilaterally symmetrical stage at some point in the lifecycle.

Protostomes include Ecdysoza and Lophotrochozoa, those that go through ecdysis, and those that do not, respectively.

EARLY CLEAVAGE IN PROTOSTOMES (vs. Deuterostomes)

SPIRAL VERSUS RADIAL CLEAVAGE.

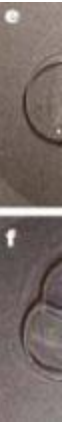
One of the most fundamental differences between Protostomes and Deuterostomes is that their early embryos have a fundamentally different pattern of early cleavage.



Deuterostomes go through an early pattern of cleavage called **RADIAL CLEAVAGE**. This pattern of cleavage is one in which the organism viewed from above (dorsal, animal pole) is essentially radial in symmetry – where a dorso-ventral slice in any plane will yield a set of mirror images.

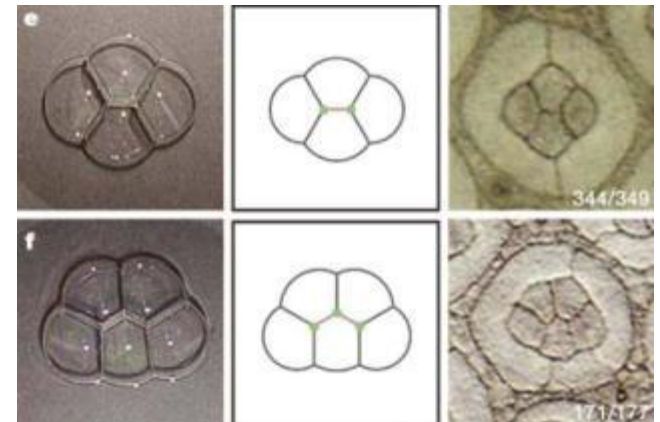
Protostomes don't have radial cleavage. Rather, they have **SPIRAL CLEAVAGE**. Spiral cleavage is an early cleavage pattern in which cleavage planes are not parallel or perpendicular to the animal-vegetal pole axis of the egg. Cleavage takes place at oblique angles, forming a “spiral” pattern of daughter blastomeres.

1. This means that daughter blastomeres touch one another in a greater number of places than those that undergo radial cleavage.
2. It has been suggested that this is the most thermodynamically stable packing option available – sort of like how soap bubble pack themselves.
3. Spirally cleaving embryos usually go through fewer divisions before gastrulation (primitive/early gut formation begins) – making it easier to track the fate of individual cells.

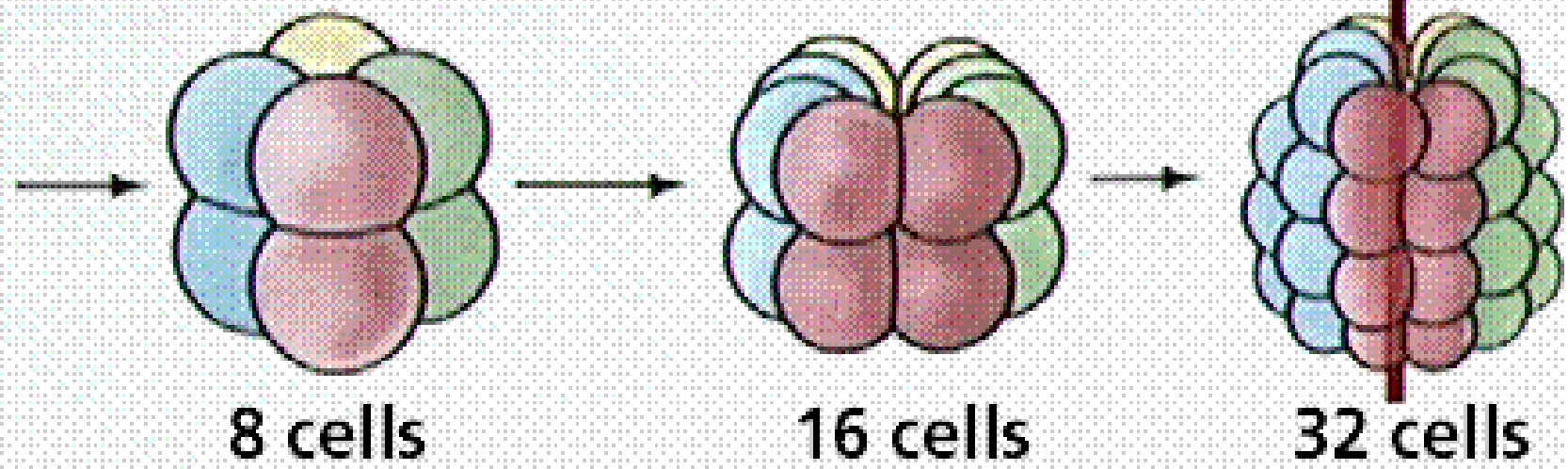


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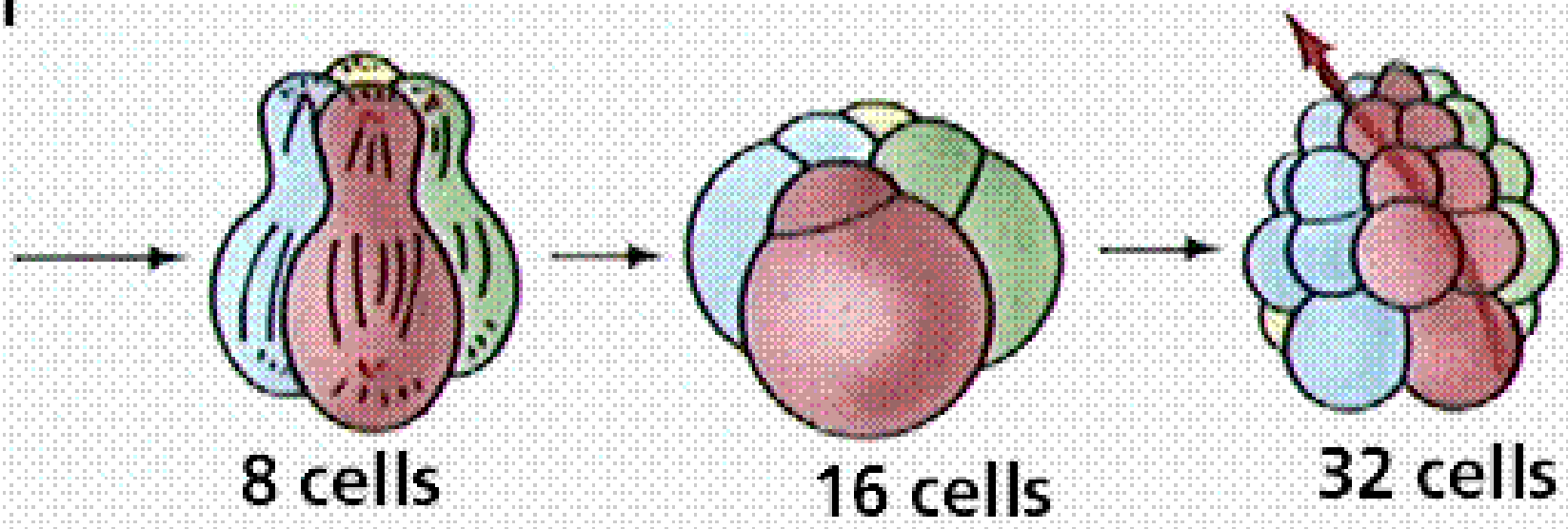
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Radial



Spiral



If you're taking notes with the PowerPoint slides, practice drawing radial versus spiral cleavage here:

EARLY CLEAVAGE IN SELECTED PROTOSTOMES:

Recall our earlier discussion of egg types (microlecithal, mesolecithal, macrolecithal). Many different egg types can be found through the diversity of protostomes.

Microlecithal eggs are found in annelids, mollusks and nematodes.

Because there is little or no yolk, there is no impediment to early cleavage. Thus, cleavage is often termed **HOLOBLASTIC**.

Insects actually store a moderate to large amount of yolk in their eggs. This means that the thickness of the yolk can impede clean cleavage, even early on in ontogeny.

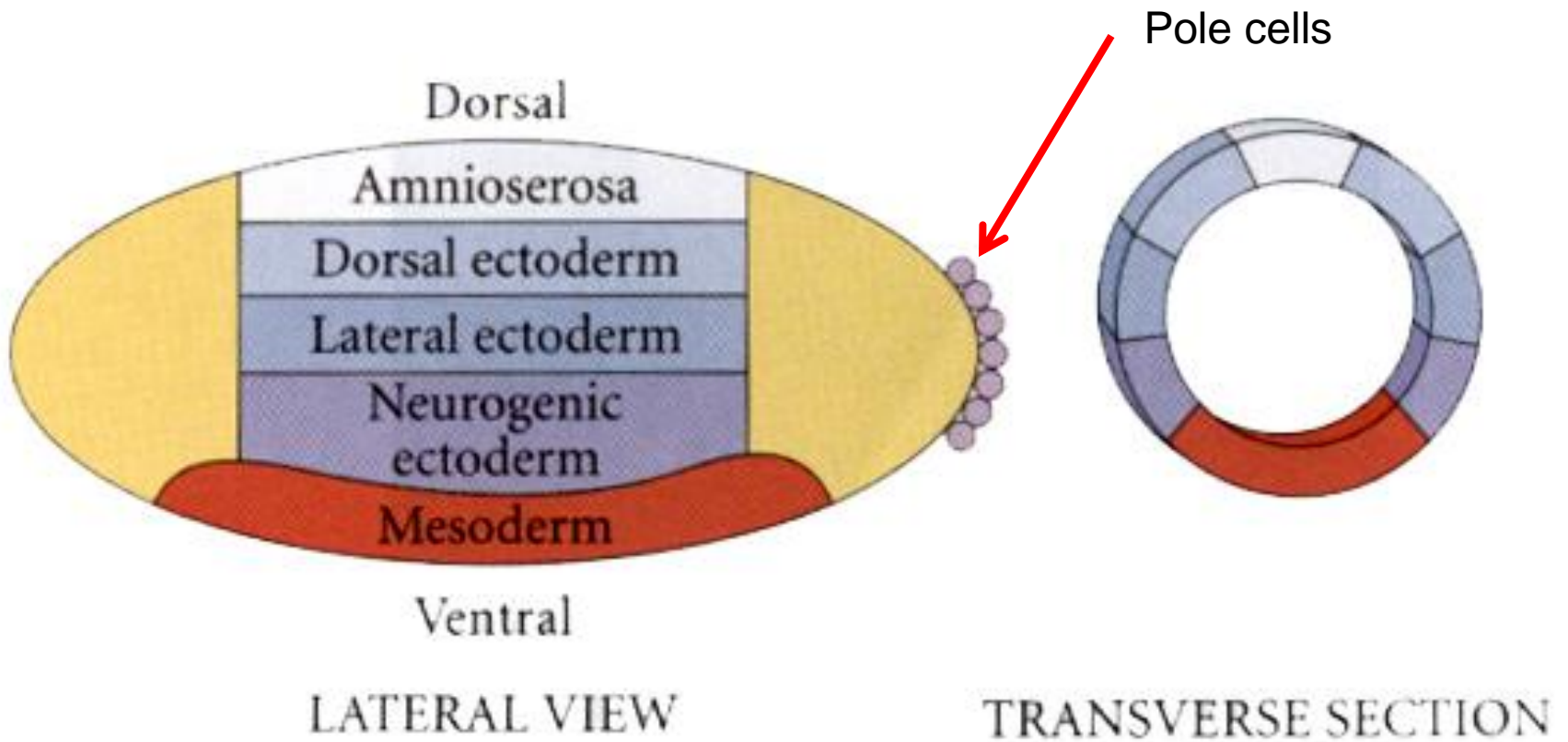
Insects tend to exhibit a condition known as **CENTROLECITHAL**, where there is a moderate to large amount of yolk, and it is concentrated in the center of the egg.

This means that although there is resistance to cleavage plane development in the center of the egg, it is easier to develop cleavage plane at the periphery of the egg – and thus early zygote. This leads to a pattern of early cleavage known as incomplete, or **MEROBLASTIC CLEAVAGE**.



Early Cleavage in a Fruit Fly, *Drosophila* (here chromatin is stained so it can be tracked).

Note: The chromosomes are replicating centrally but there is too much yolk to allow cleavage, so there are multiple nuclei centrally. They then migrate to the periphery, and only there does the meroblastic cleavage (eventually) take place.

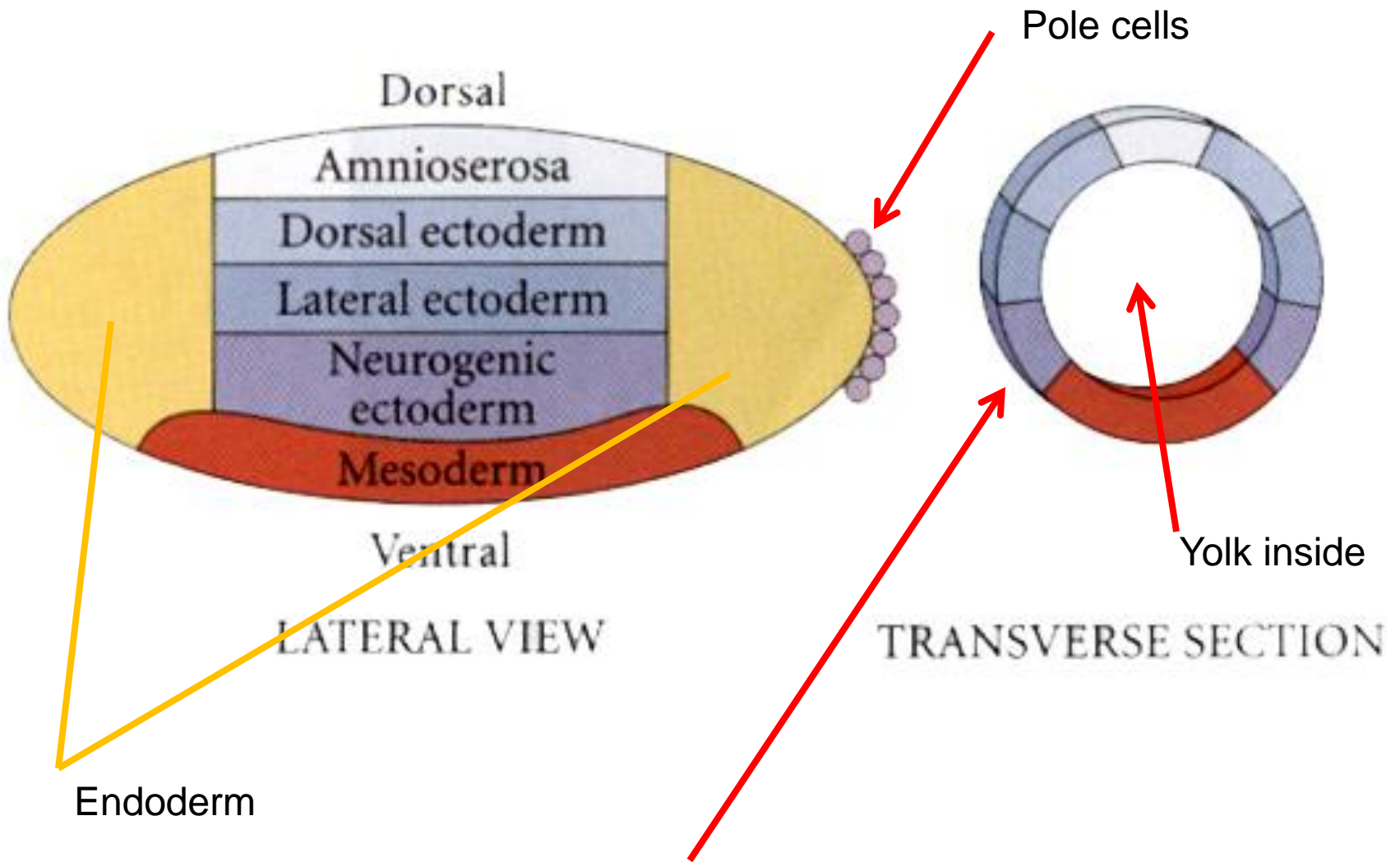


“Fate Map” of a developing insect (representative protostome).



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In cross section: single layer of cells known as **CELLULAR BLASTODERM**.

During the ninth mitotic division, about five nuclei reach the posterior of the embryo. Once surrounded by their own cell membranes, they eventually become **POLE CELLS**, the cells that will give rise to future gametes.

It is only after cell division 12 or 13 that the membrane of the egg finally starts giving meroblastic infolding to define individual cells. This creates a single layer of cells surrounding the egg – known as the **CELLULAR BLASTODERM**.

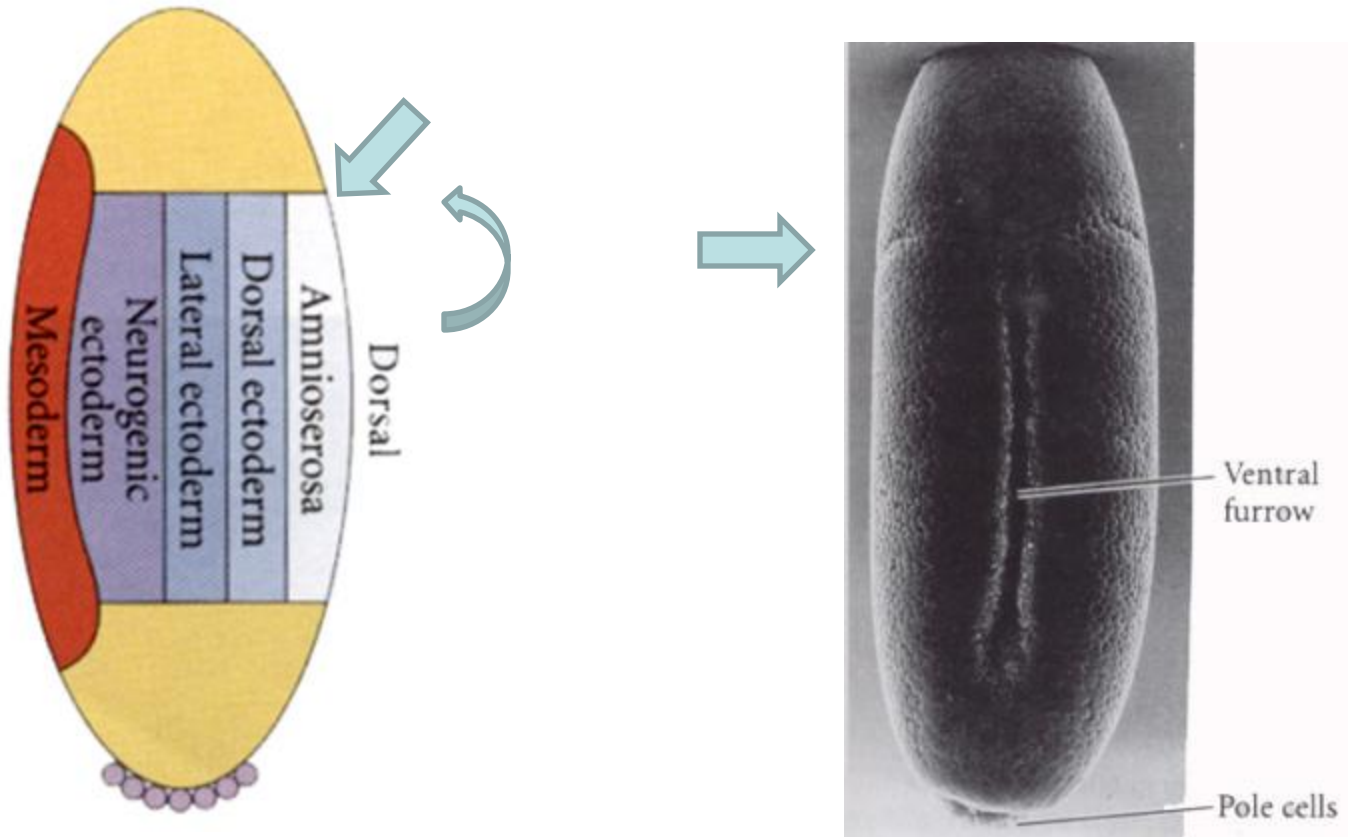
Technically, the formation of the cellular blastoderm is equivalent to the stage in deuterostomes known as the “blastula stage” – or the hollow ball stage – a stage essentially present to deal with surface/volume constraints.

Although the deuterostome blastula stage is a hollow ball of cells, the equivalent in insects is not surrounding a fluid-filled space, but yolk.

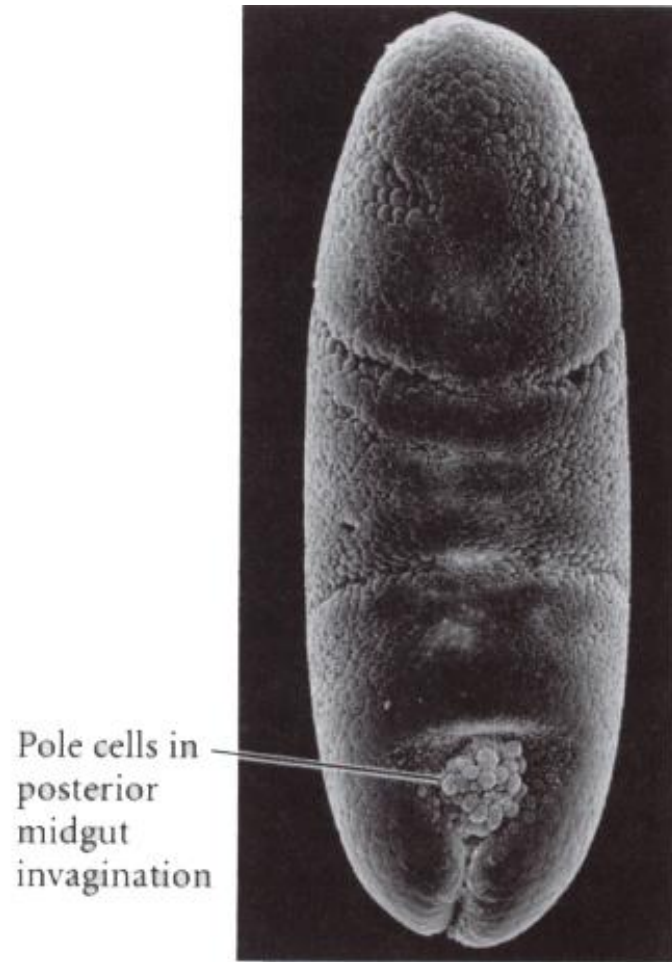
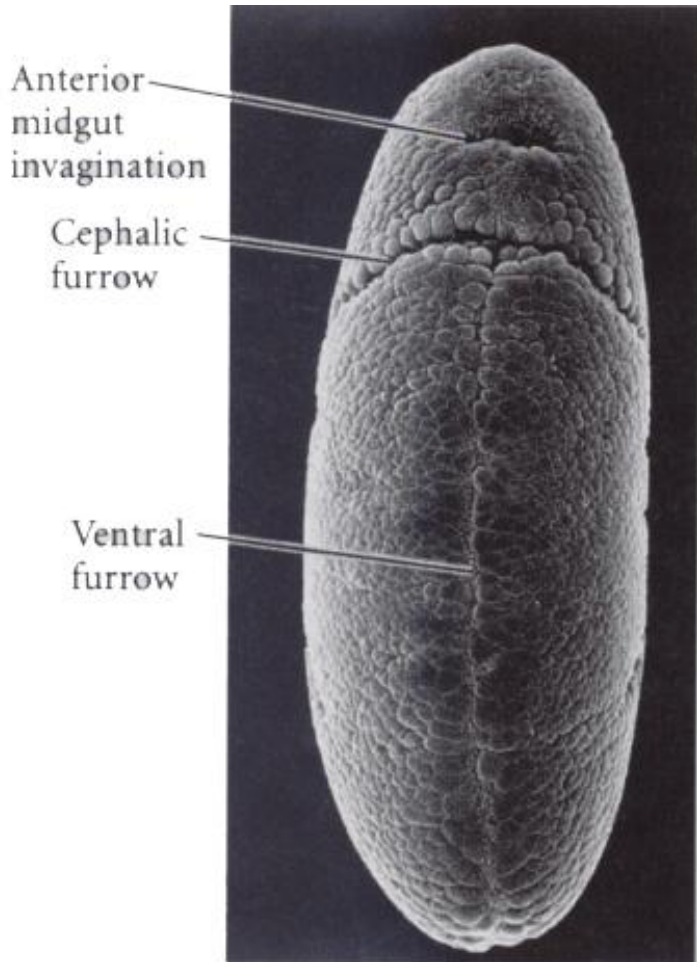
The next stage after the blastula stage is ‘GASTRULATION’ – or gut formation. Most types of gut formation involve some kind of involution or inner migration of cells to create an inner gut tube within the outer body tube. Note that this isn’t easy with the virtually yolk/solid *Drosophila* embryo.

PROCESS OF GASTRULATION IN *DROSOPHILIA*

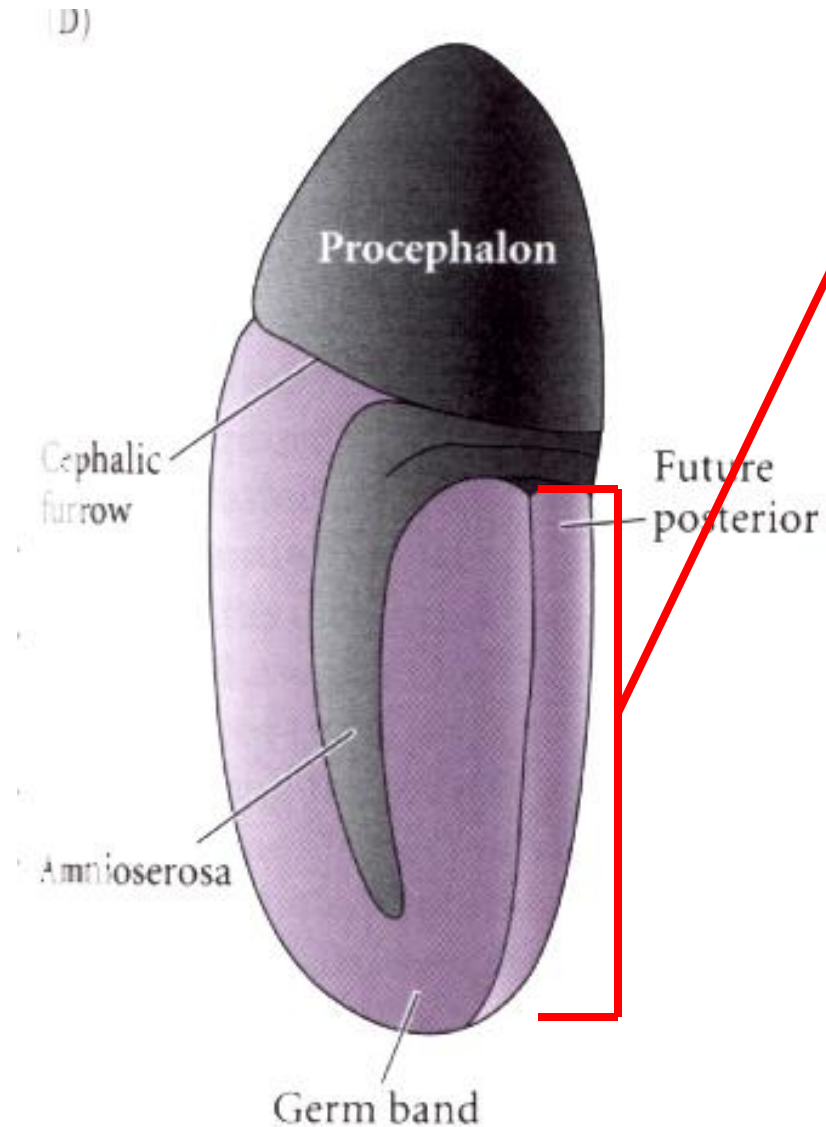
1. Cell movements, during gastrulation segregate the first distinct prospective endoderm, ectoderm, and mesoderm.
2. Prospective mesoderm invaginates to form the ventral furrow. This will eventually pinch off within to become a ventral tube in the body.



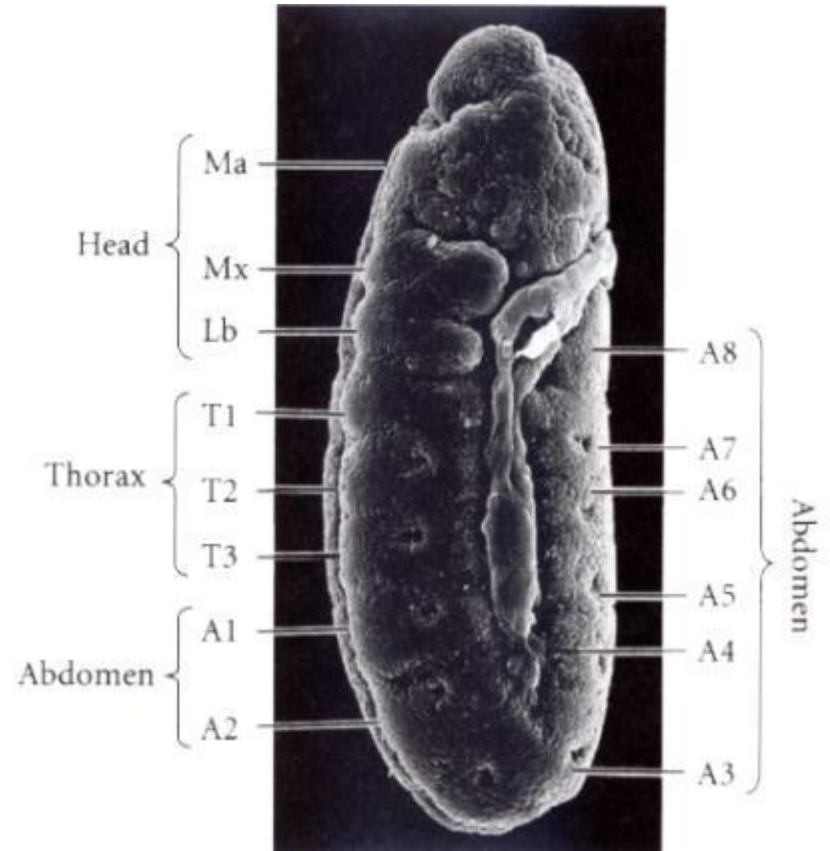
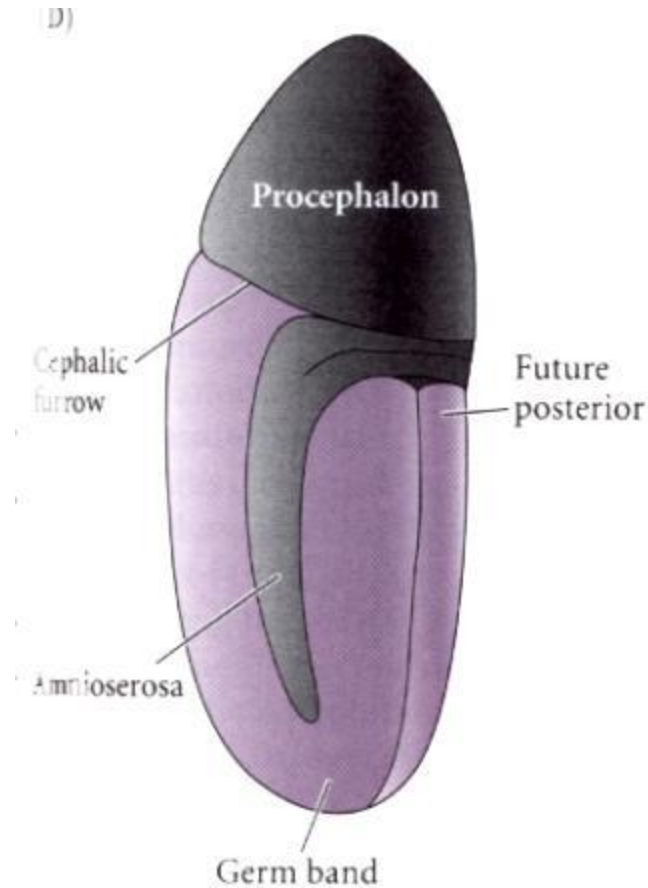
3. Prospective endoderm invaginates to generate two pockets at the anterior and posterior ends of the ventral furrow. Pole cells are internalized at the posterior end with the endoderm. At the head end, the endodermal cells invagination generates the cephalic furrow.



4. On surface of embryo, ectodermal and mesodermal cells extend, and migrate toward one-another in the ventral midline – this generates the **GERM BAND**. The germ band will give rise to pretty much all the cells that will form the trunk of the insect.



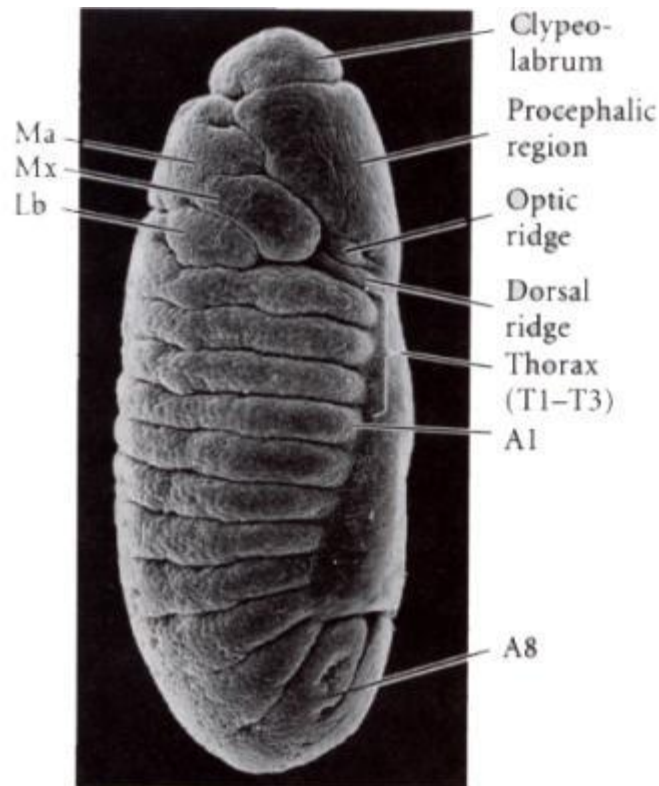
5. As the germ band matures, segmentation begins to develop too. The entire embryo is still encased in an egg case. So, the germ band can't simply extend – it is forced to bend and continue up around back toward the head.*



6. *Throughout this course, the shape of egg and yolk constraining development will be a theme.

7. When the germ band is in its extended, mature position, several significant morphogenetic events occur:

- Beginning of organogenesis
- Significant segmentation
- Segregation of imaginal discs (structures that will give rise to adult structures)

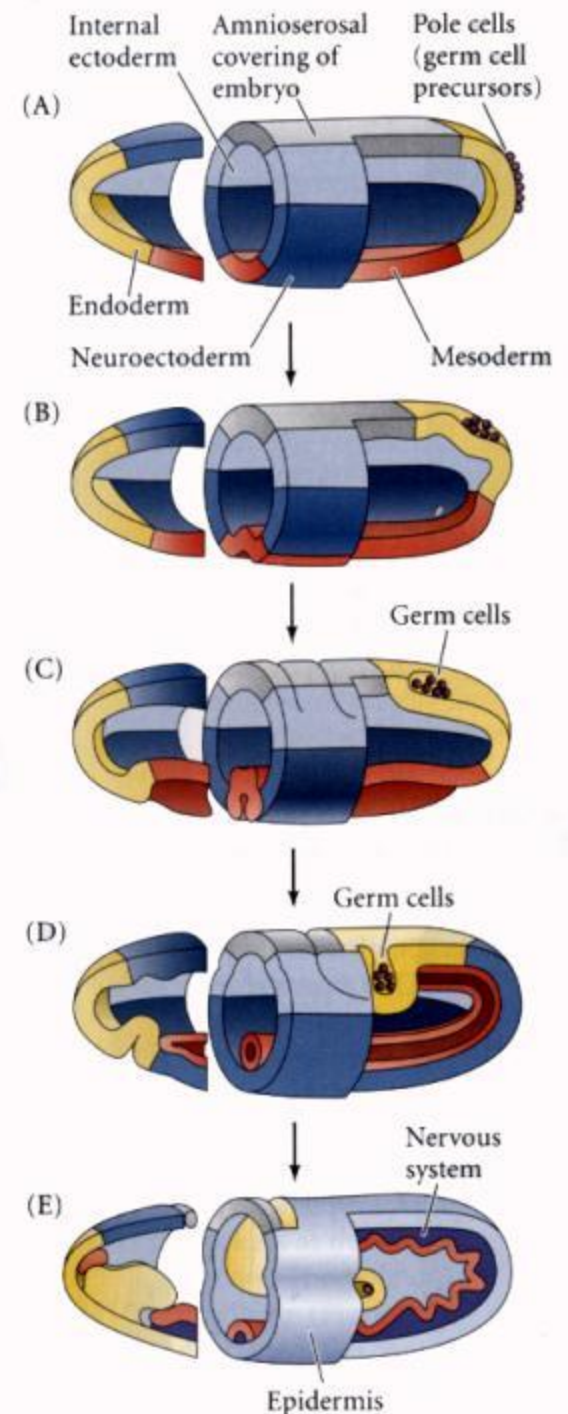


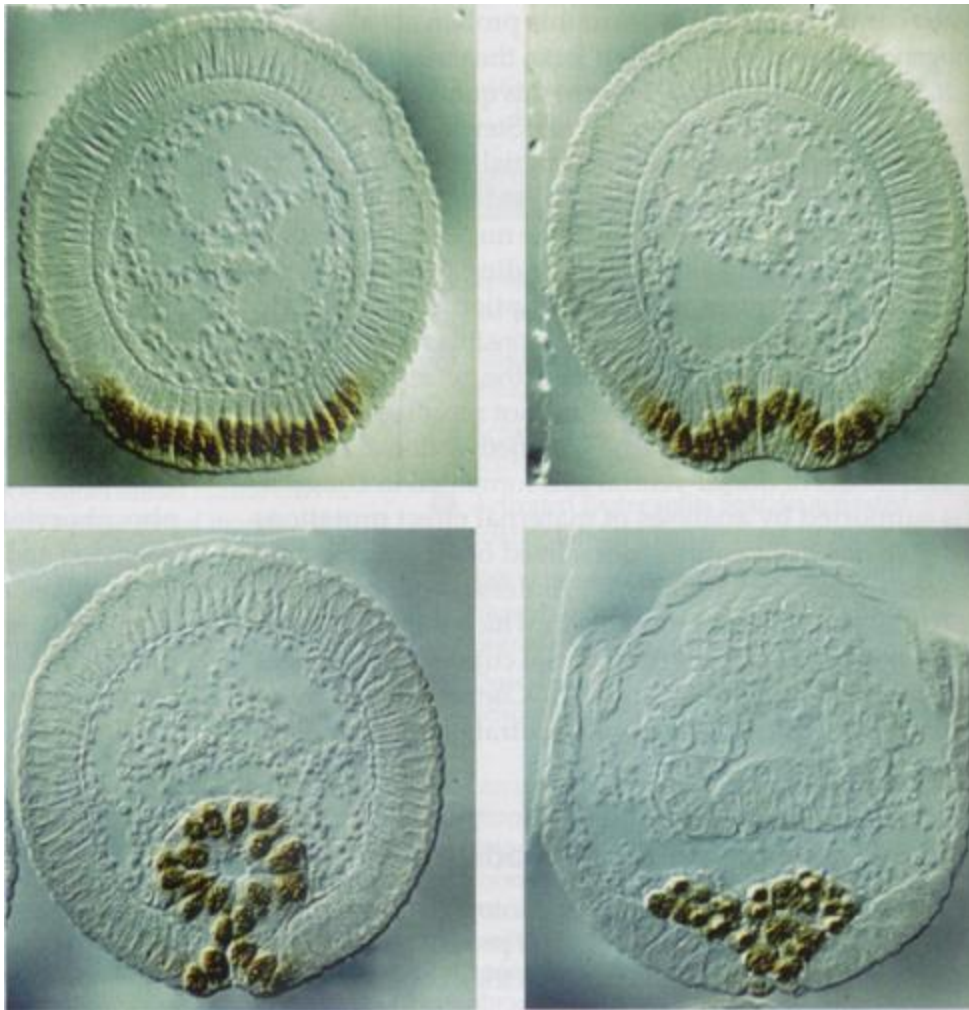
Color-coded fate maps show invagination of the mesoderm.

The furrow formation, zipping, and sinking in of the mesoderm is very similar in movement to the formation of the chordate neural tube.

Note also segregation of the pole cells.

After invagination of mesoderm, cells of nervous system follow in (recall previous location on fate map).

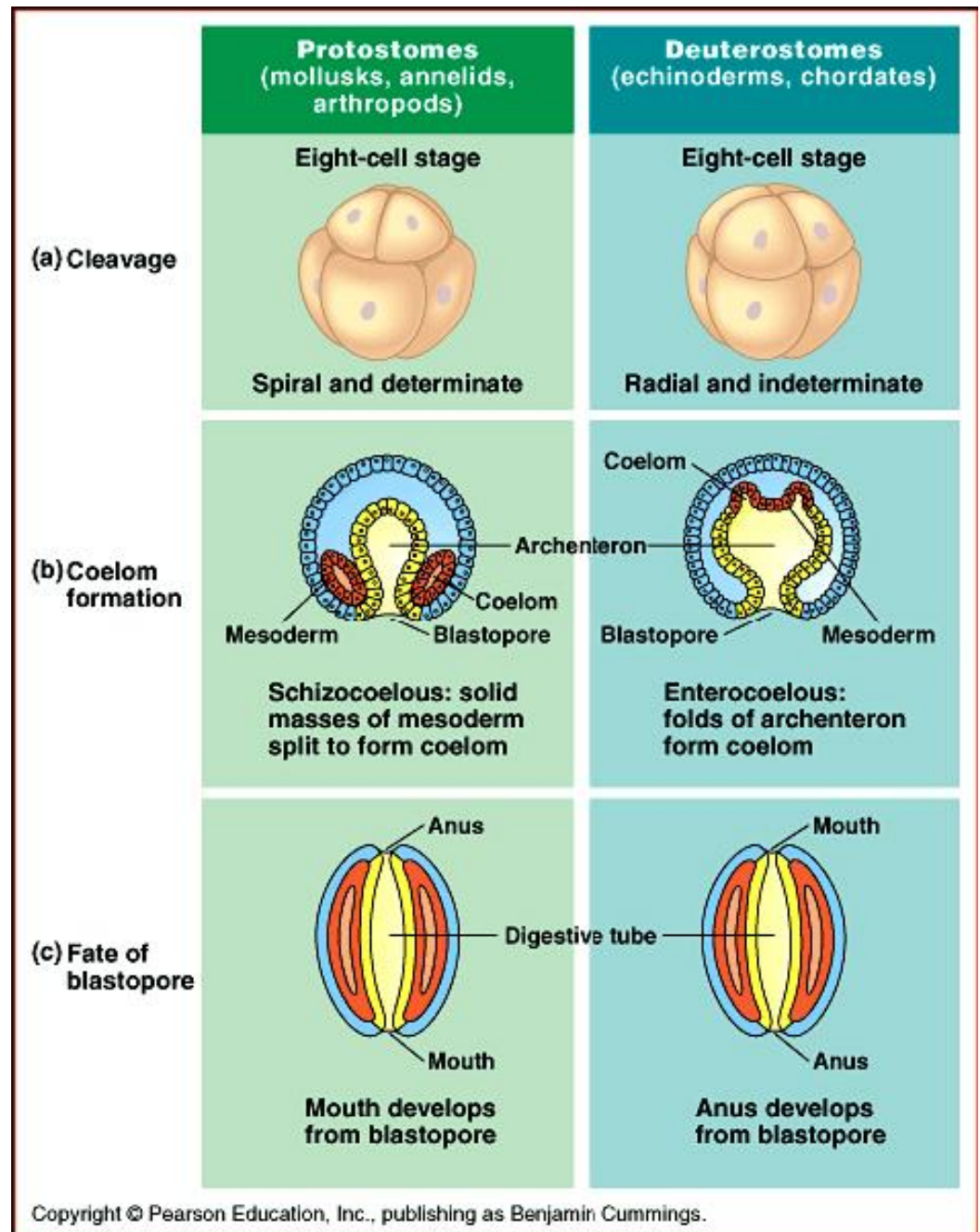




Invagination of mesodermal cells during gastrulation. These cells are specified by a particular protein – here called **Dorsal Protein**.

After invagination of mesoderm, the solid mass of mesoderm will split to make a space that eventually becomes the coelom.

Splitting of solid mass of mesoderm to make a coelom is called **SCHITZOCOELOUS COELOM FORMATION.**



General body plan of adult *Drosophila* is same as the embryo and larva:

- Distinct head and tail
- Intervening body segments
 - Thorax: 3 segments
 - #1 – legs only
 - #2 – leg and wings
 - #3 – legs and balancing organs
 - Abdomen: 8 segments

