

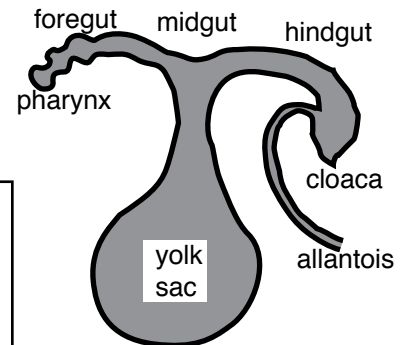
Digestive System

NOTE: The digestive system consists of the: mouth (oral cavity); pharynx; esophagus; stomach; small intestine; colon and cecum; rectum; anal canal; and the liver, pancreas, and salivary glands.

Development of a head process and tail process, including the ventral merger of lateral body folds, transforms splanchnopleure into a foregut and a hindgut, leaving a midgut region that is continuous with the yolk sac.

NOTE: Foregut becomes pharynx, esophagus, stomach, cranial duodenum, and liver and pancreas. Midgut becomes the remaining small intestines, cecum, ascending colon, and part of the transverse colon. Hindgut becomes transverse and descending colon and a cloaca which forms the rectum and most of the anal canal.

In the abdomen, derivatives of the foregut, midgut, and hindgut are those structures supplied by the celiac, cranial mesenteric, and caudal mesenteric arteries, respectively.

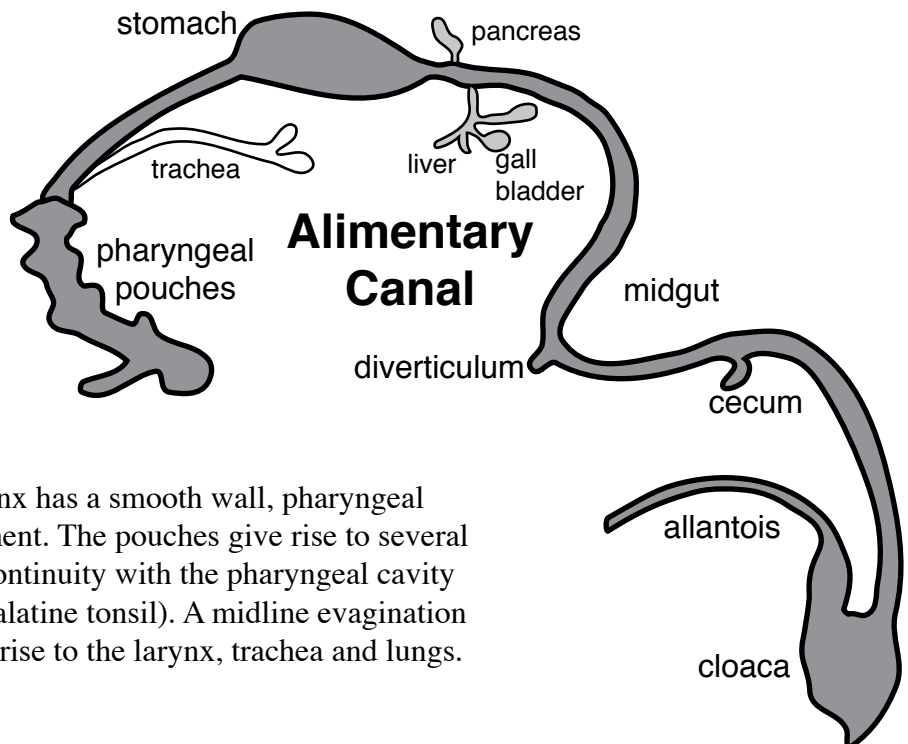


Endoderm gives rise to the epithelial lining of the digestive tract, while splanchnic mesoderm forms connective tissue and smooth muscle components of the digestive tract wall; except that ectoderm forms the epithelial lining of the proctodeum (caudal end of anal canal) and stomadeum (mouth & salivary glands — parotid, zygomatic, labial & buccal).

Pharynx...

The adult pharynx is a common respiratory-digestive chamber. Initially, the pharynx is bounded cranially by an *oropharyngeal membrane*. The membrane degenerates early, allowing the pharynx to communicate with the oral and nasal cavities, and enabling migration of tongue musculature into the oral cavity.

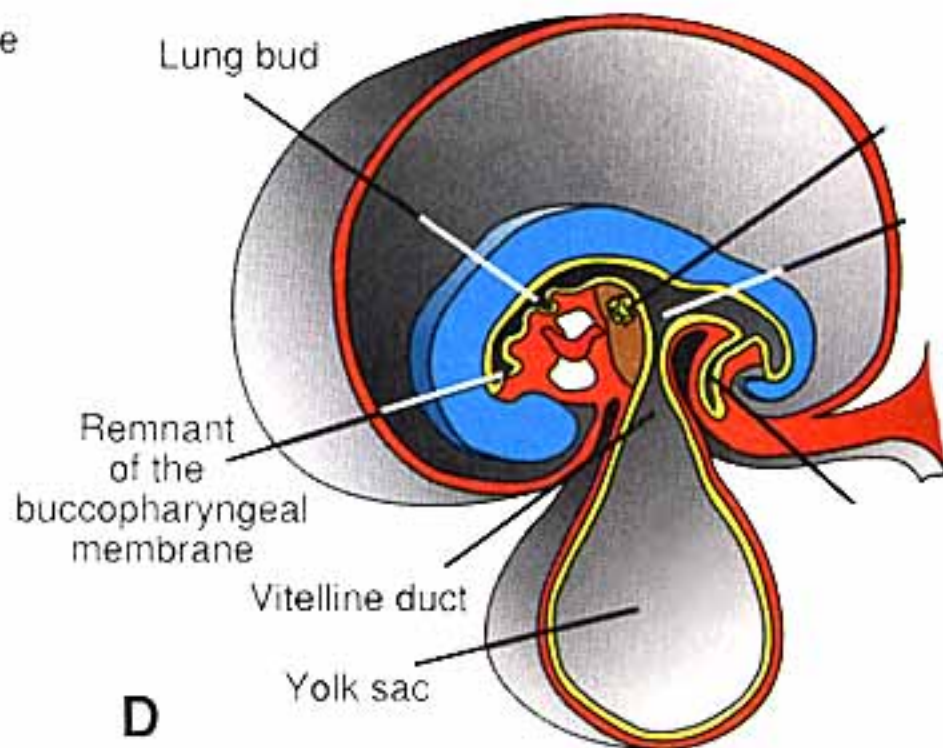
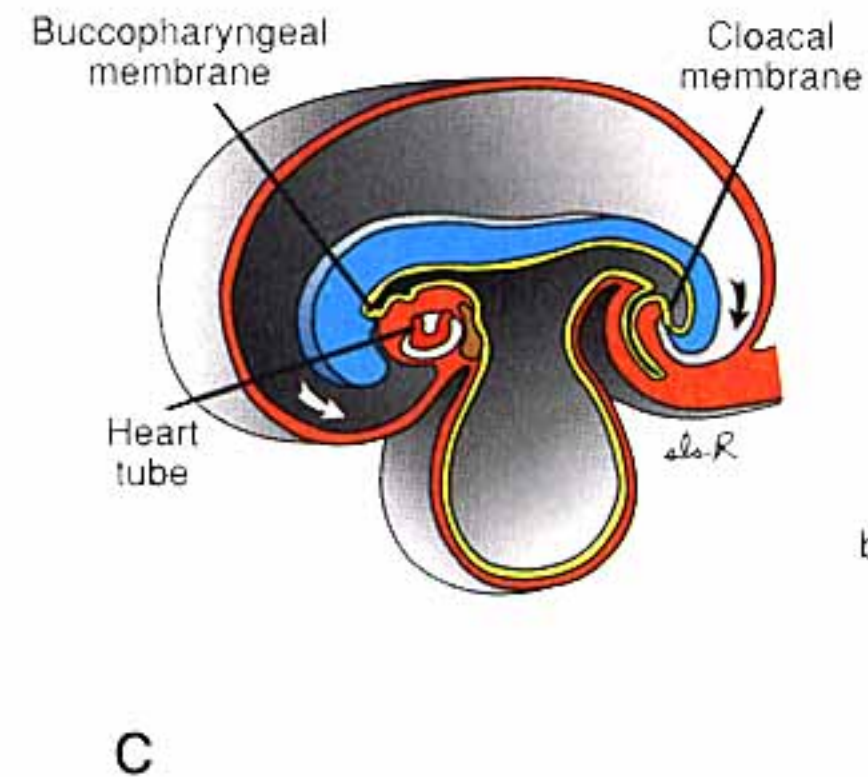
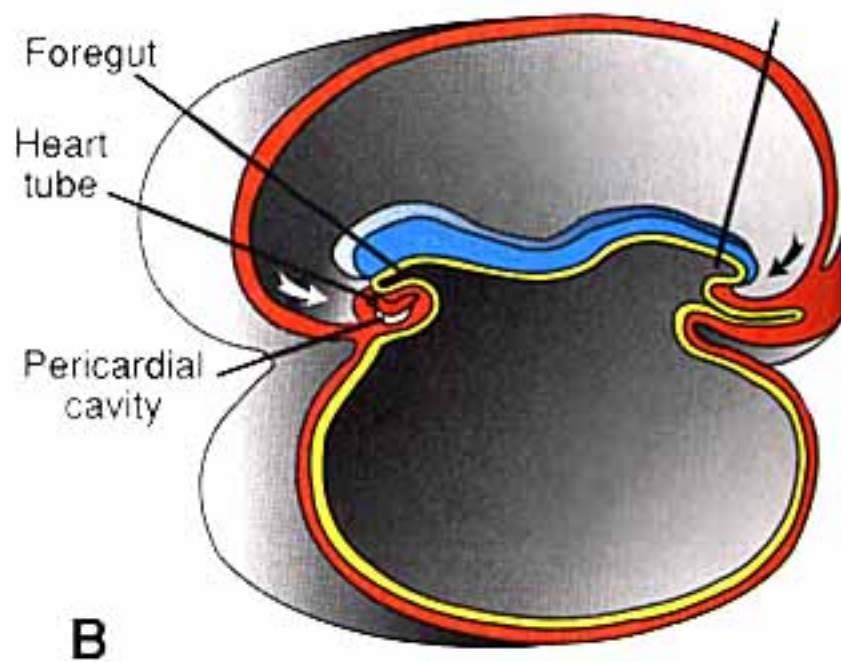
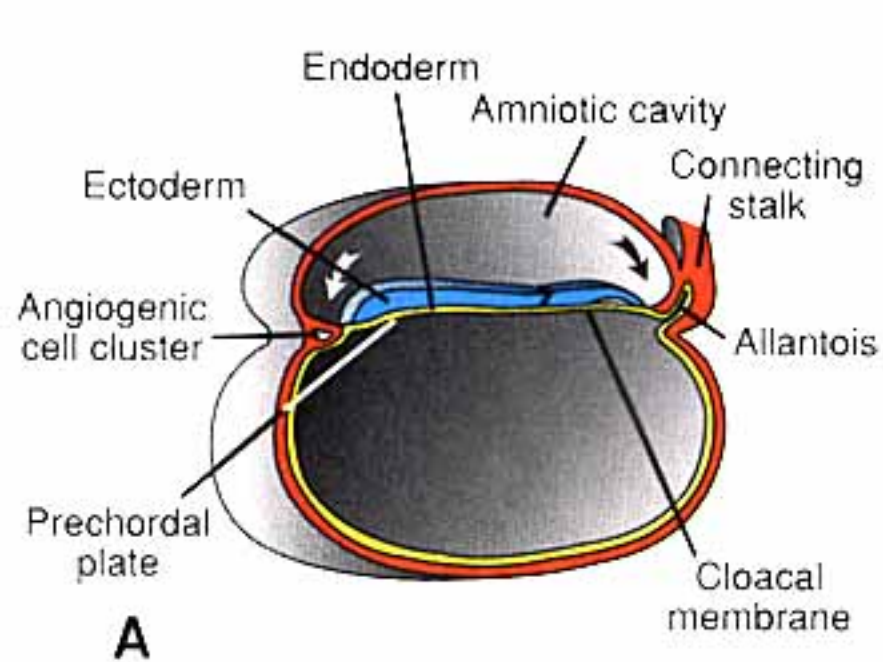
Although the adult pharynx has a smooth wall, pharyngeal pouches appear during development. The pouches give rise to several structures, two of which retain continuity with the pharyngeal cavity (auditory tube and fossa of the palatine tonsil). A midline evagination of the floor of the pharynx gives rise to the larynx, trachea and lungs.

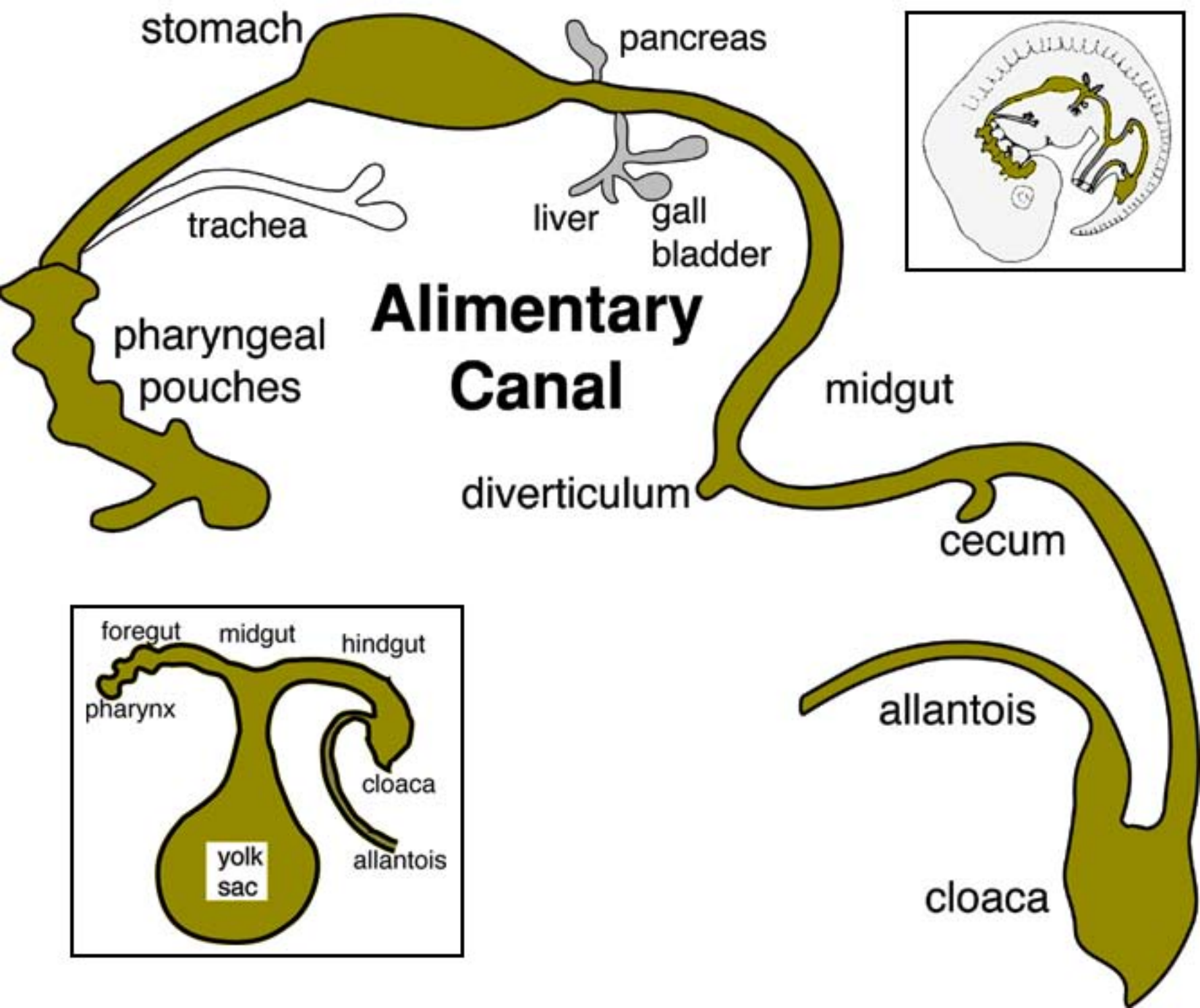


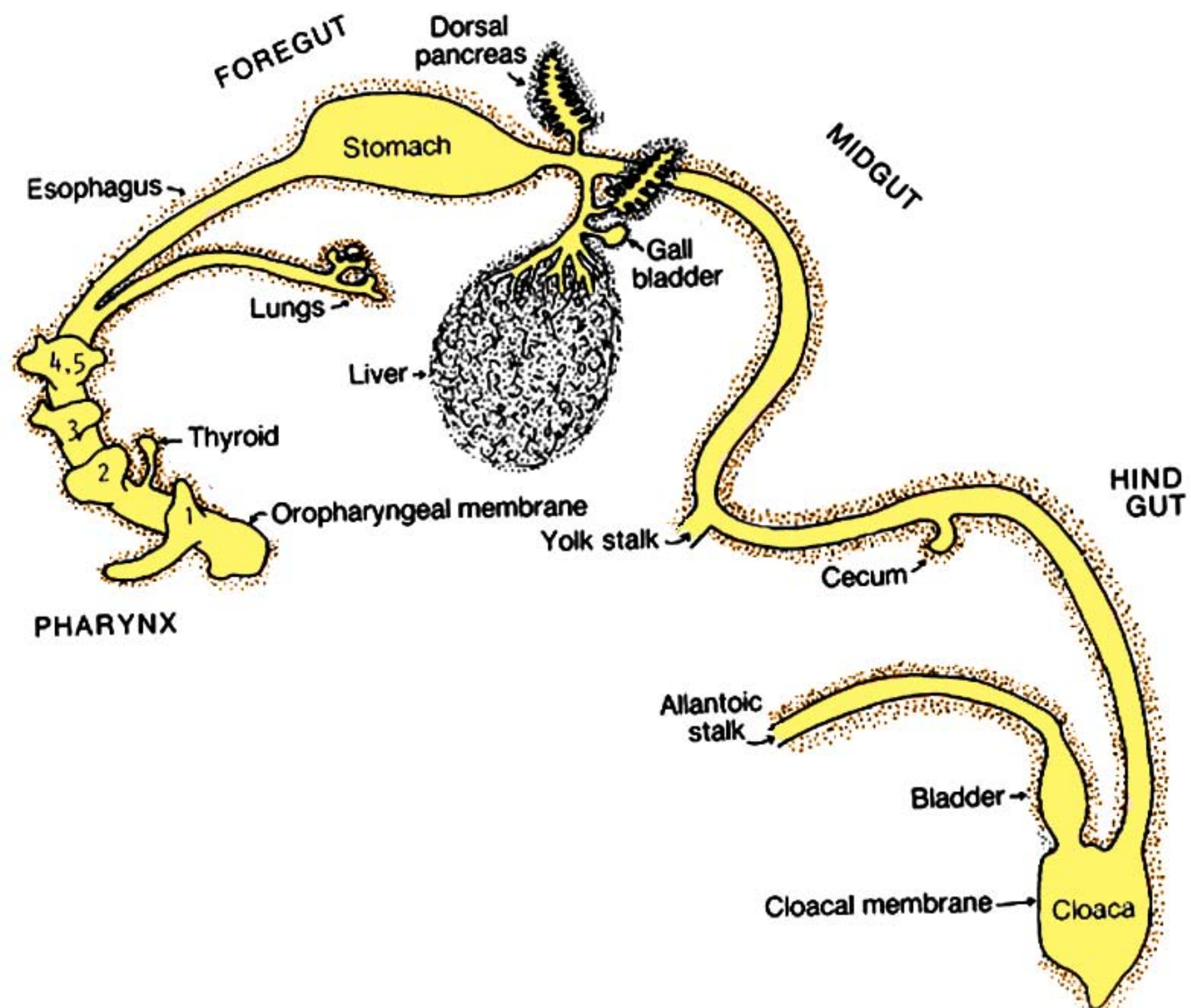
Esophagus...

The esophagus develops from foregut, caudal to the pharynx. Its principal morphogenic development is elongation.

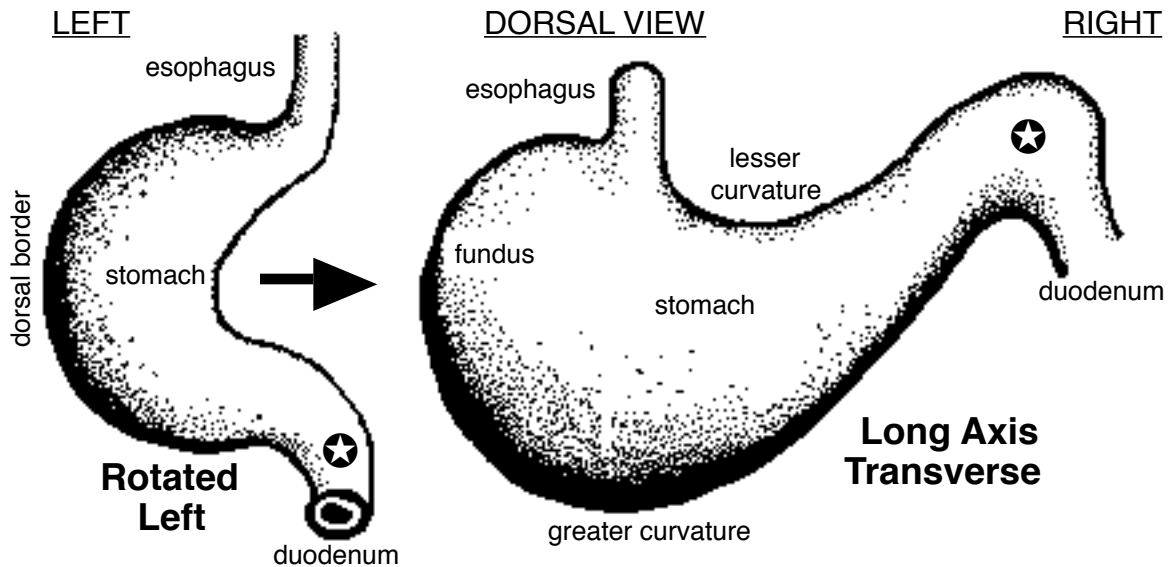
Skeletal muscle associated with esophagus & pharynx is derived from somites that migrate to the pharyngeal arches IV-VI (innervation is from vagus nerve). Esophagus is coated by skeletal muscle throughout its length (dog, ruminants), to the diaphragm (pig), to the mid-thorax (cat, horse, human), or not at all (avian).







SIMPLE STOMACH DEVELOPMENT



Stomach (simple stomach)...

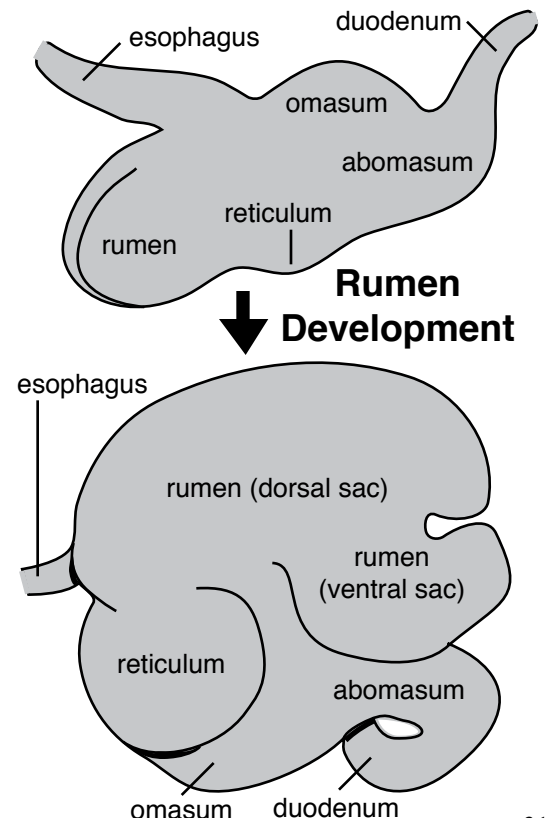
Most domestic mammals have a simple stomach (in contrast, ruminants have a complex stomach with multiple compartments). The simple stomach develops from a tubular segment of foregut that undergoes the following morphogenic changes:

- growth is more rapid dorsally than it is ventrally; the tube becomes convex dorsally (the future greater curvature) and concave ventrally (future lesser curvature);
- the tube rotates 90° to the left (dorsal faces left & ventral faces right);
- the long axis becomes transverse as growth of the liver pushes the cranial end of the stomach to the left side (the greater curvature drops ventrally when the stomach is filled);
 - growth along the cranial aspect of the greater curvature is greater than along the caudal aspect — this produces a fundus region (to the left);
 - endoderm, which forms the epithelial lining of the stomach, differentiates into cells types that vary regionally among species.

Ruminant stomach...

The ruminant stomach consists of three compartments lined by stratified squamous epithelium (rumen, reticulum, and omasum) and one glandular compartment (abomasum). The early development of the ruminant stomach is the same as the simple stomach.

The *rumen* develops as an expansion of the fundus, and a caudoventral pocket of the developing rumen forms the *reticulum*. The *omasum* develops as a bulge along the lesser curvature. The rest of the stomach becomes *abomasum*. Later in development the rumen is “flipped” caudally so it comes to lay on top of the abomasum with the reticulum situated cranially.



Right

RIGHT

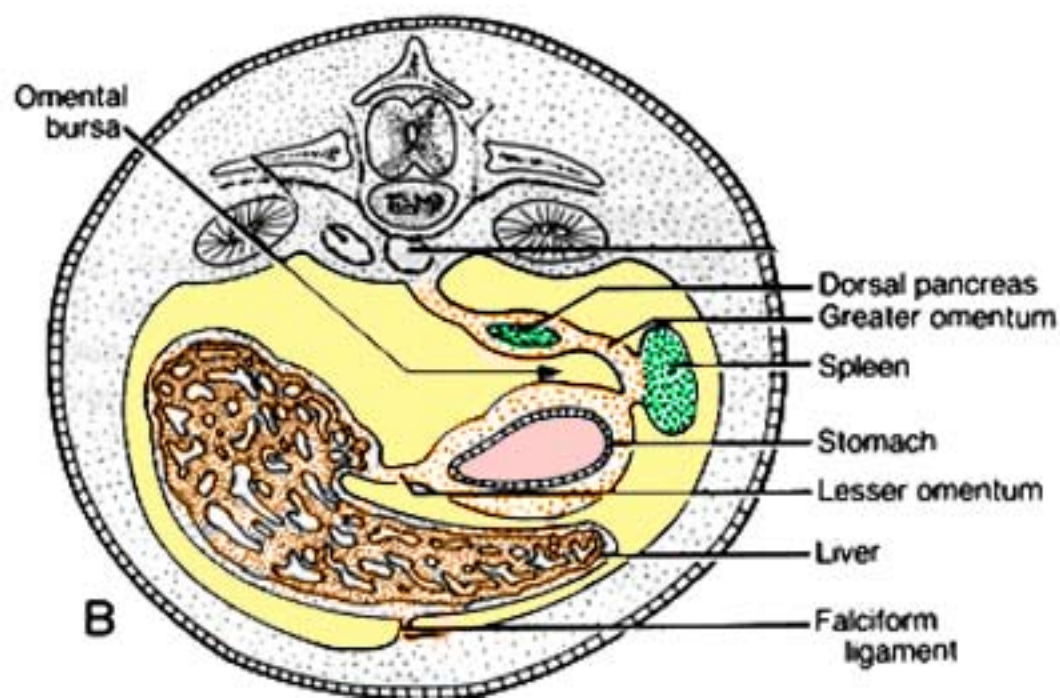
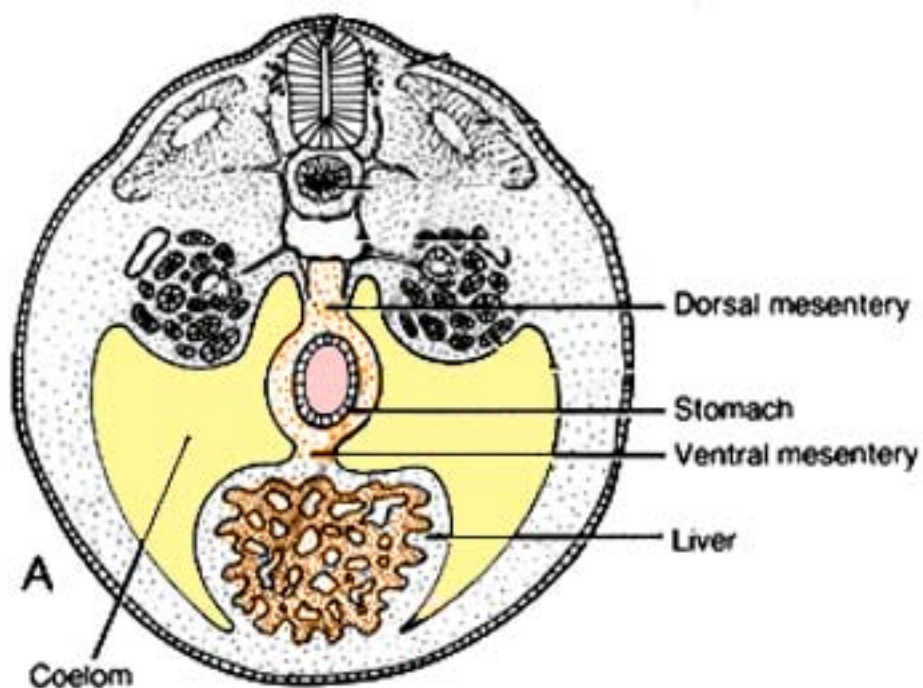
LEFT

Left

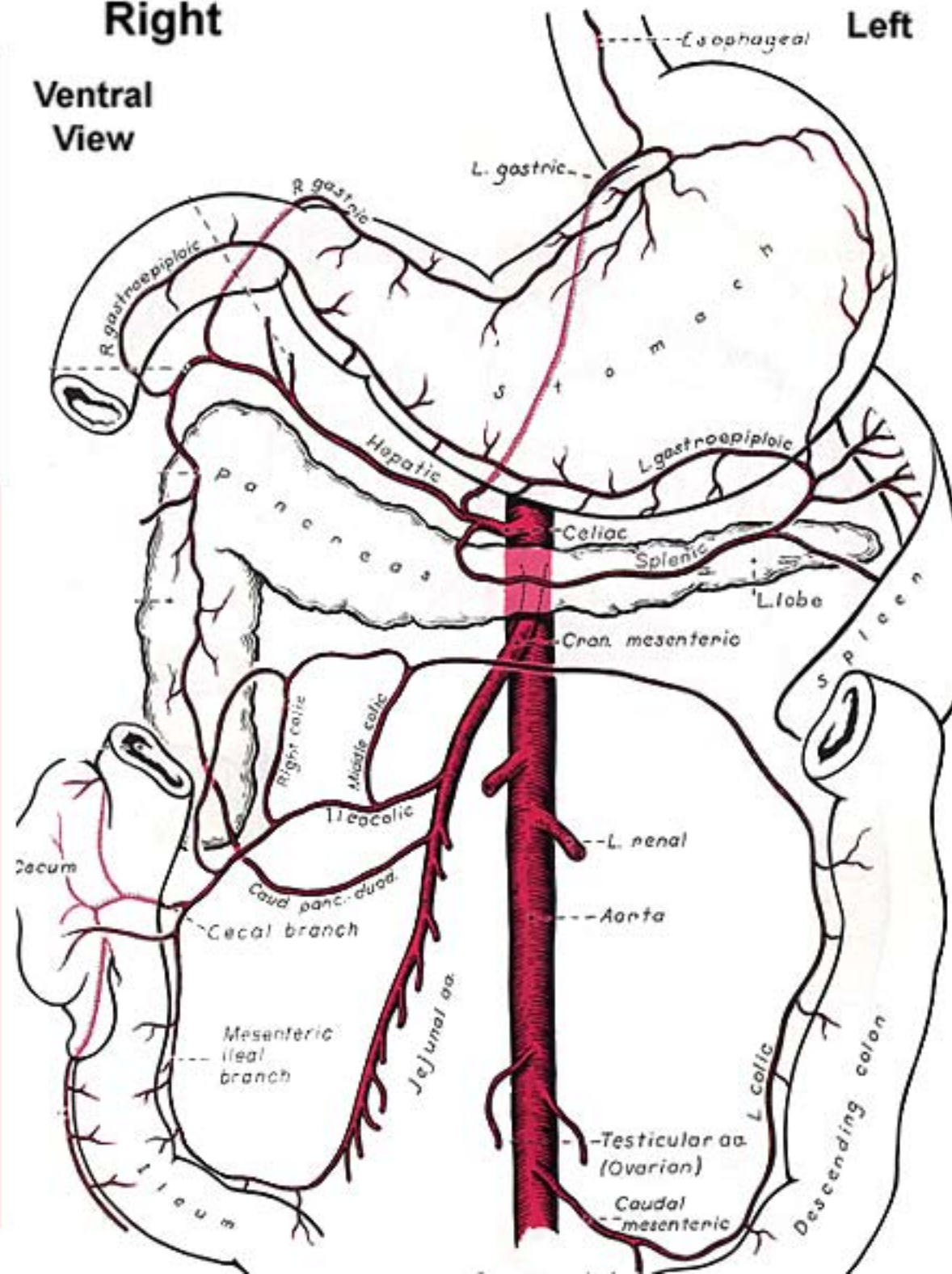
Right

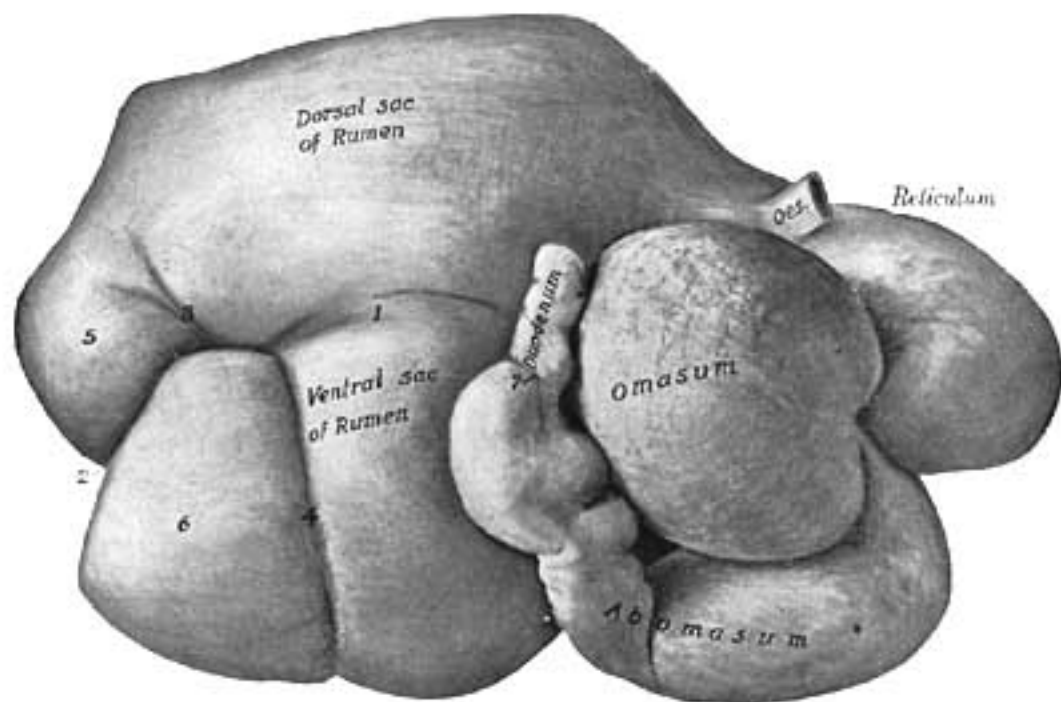
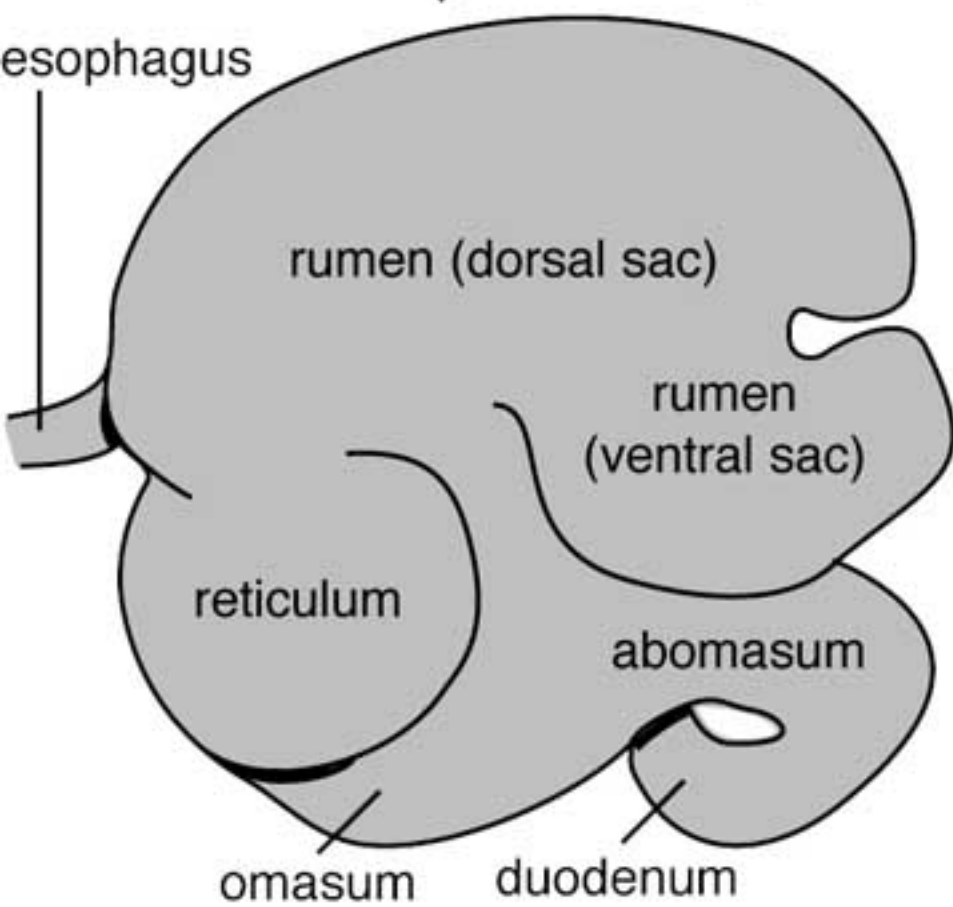
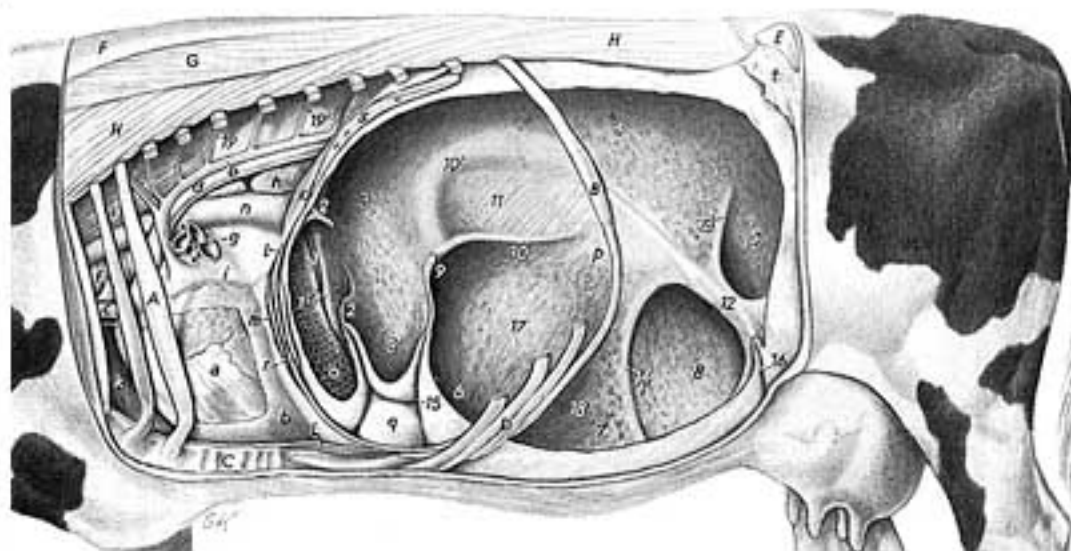
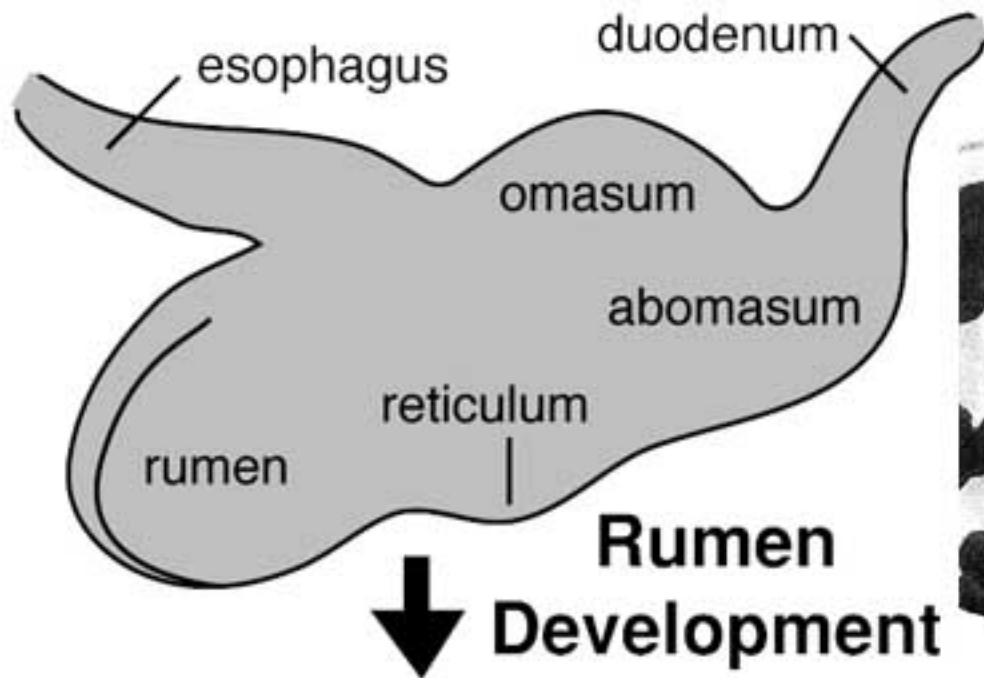
Left

Cranial
View

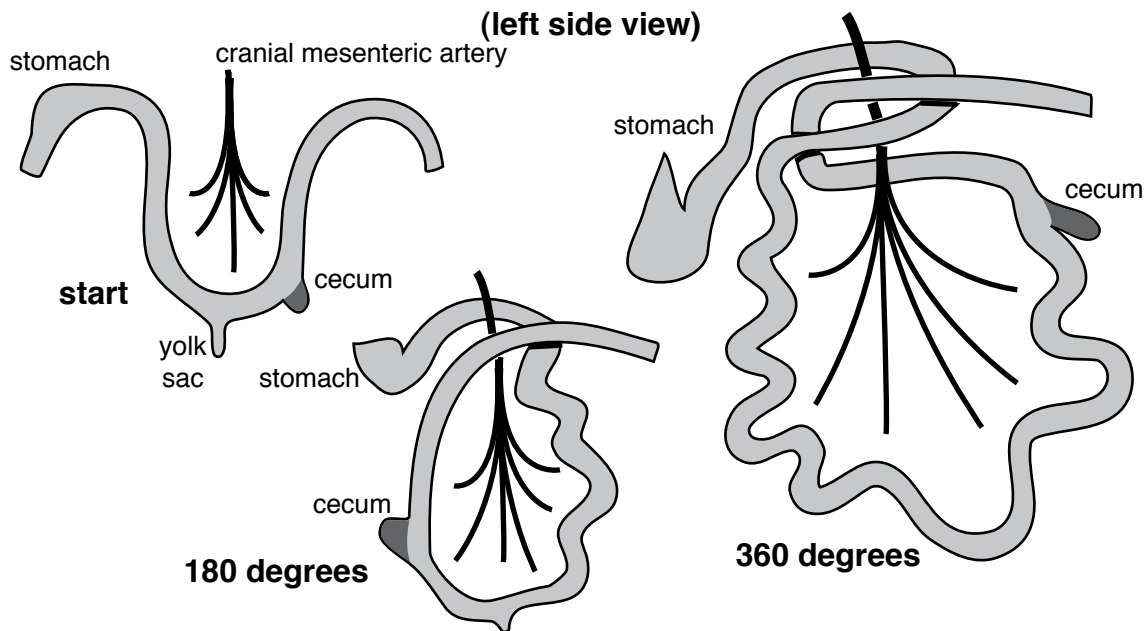


Ventral
View





Rotation of Gut Around Cranial Mesenteric A.



Intestinal tract...

NOTE. The intestinal tract consists of: duodenum (descending & ascending), jejunum, ileum, colon (ascending, transverse, & descending), cecum (diverticulum at the beginning of the colon), rectum, and anal canal.

In addition to elongation, the following morphogenic events occur:

- elongation of the midgut (where the yolk sac is attached) causes the midgut to form a loop that herniates into the coelom of the umbilical stalk;
- the loop rotates approximately 360° around the cranial mesenteric artery (former right vitelline a.), the rotation is clockwise as viewed dorsally (freedom to rotate is the result of lost yolk sac attachment and elongation of the cranial limb of the loop);
- the caudal limb of the loop develops a diverticulum, the future cecum. As the embryo grows, the loop returns to the embryonic coelom (abdominal cavity).

The intestinal tract and esophagus normally undergo atresia (occluded lumen) during development as a result of epithelial proliferation. The *atresia* is temporary. Recanalization occurs by formation of vacuoles that coalesce to form the ultimate lumen. Persistent atresia (failure to re-canalize) or stenosis (narrow lumen) is a congenital anomaly that can occur at localized sites anywhere along the esophagus or intestines.

Failure of the yolk sac to detach from the midgut (jejunum) can result in either a diverticulum of the jejunum, a fistulous (hollow) cord to the umbilicus, or a fibrous connection between the jejunum and umbilicus. Each of these can be a source of colic.

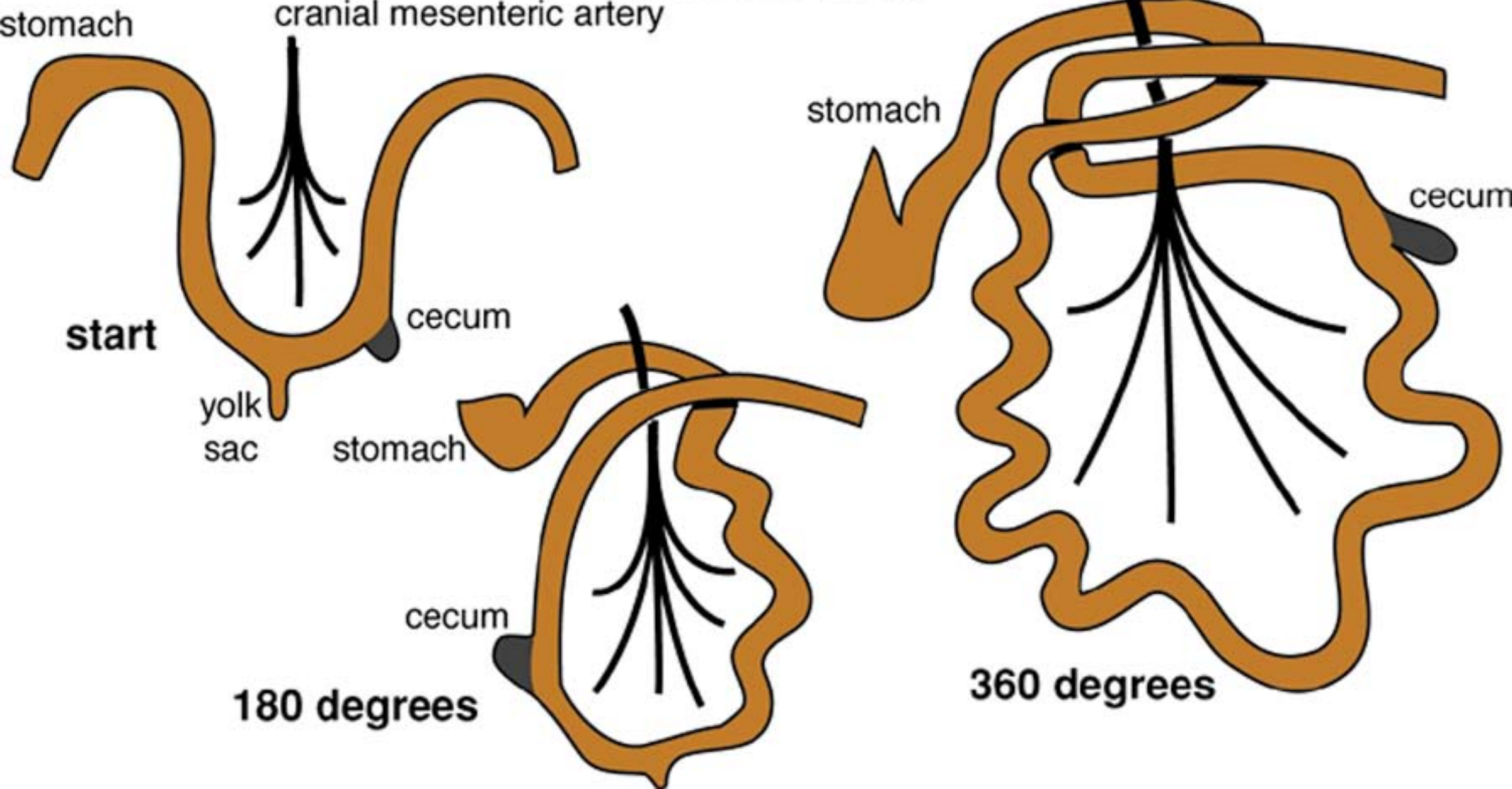
Additional intestinal events in some species...

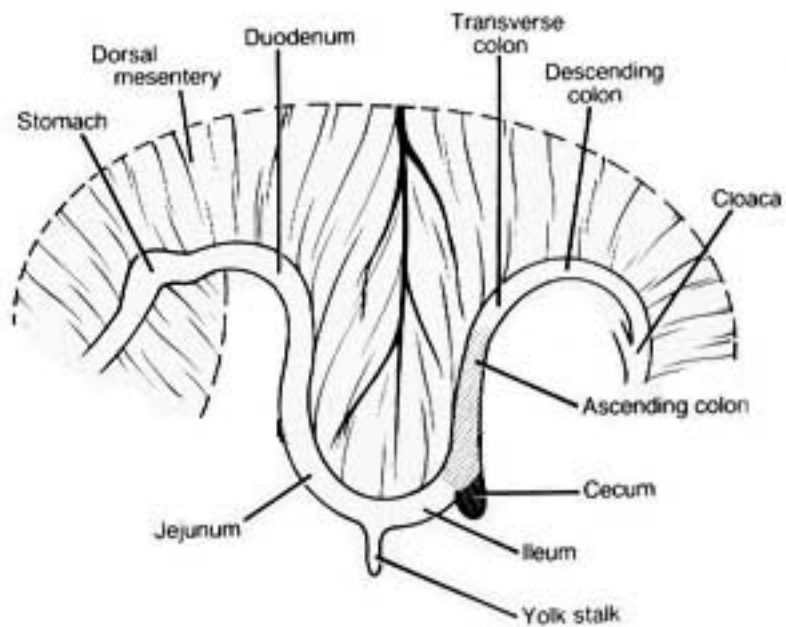
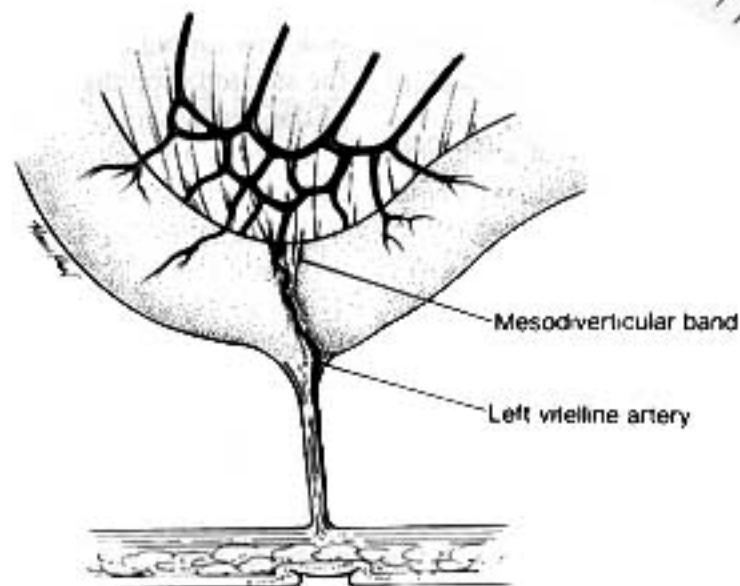
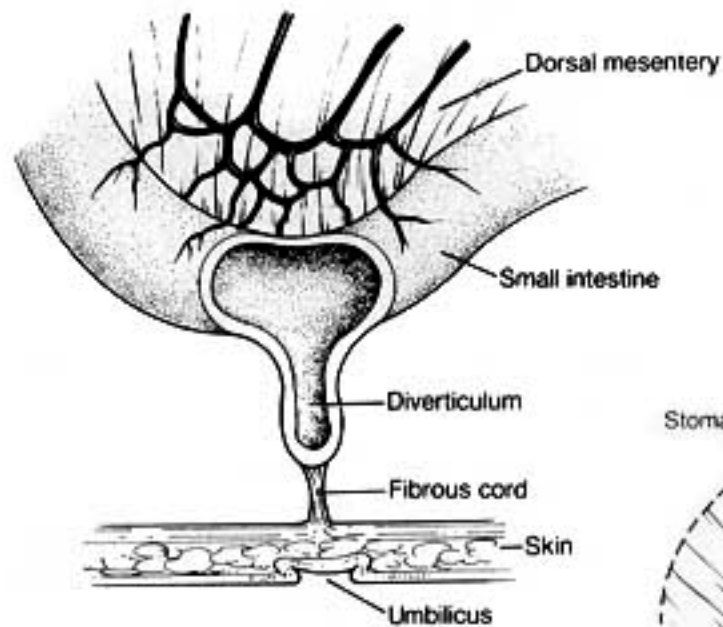
a secondary loop (of ascending colon) forms distal to the cecum (see following illustration):

- in pig and ruminant—the secondary loop coils (forming the spiral colon);
- in horse—the secondary loop bends on itself; also the cecum enlarges so that the proximal colon is incorporated within the cecum.

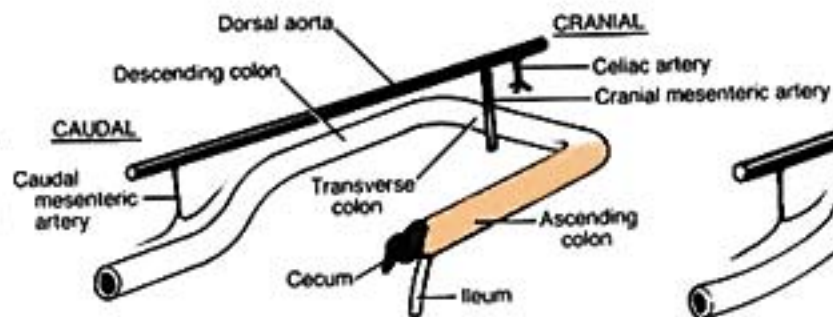
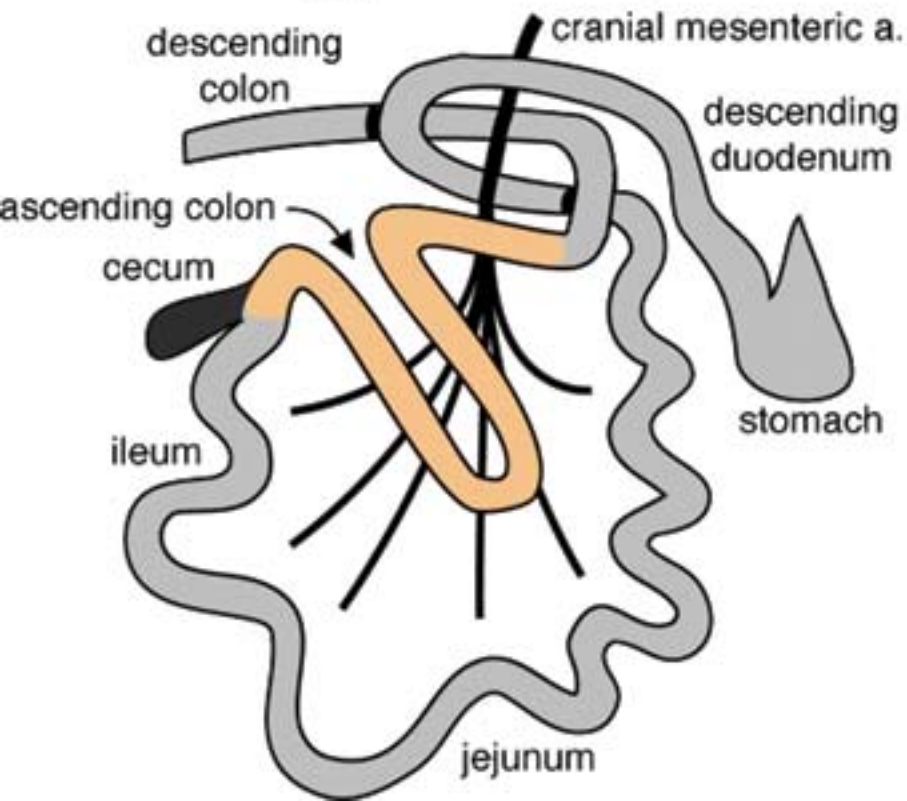
Rotation of Gut Around Cranial Mesenteric A.

(left side view)

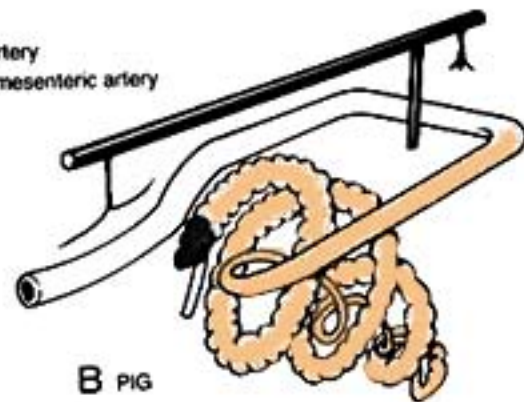




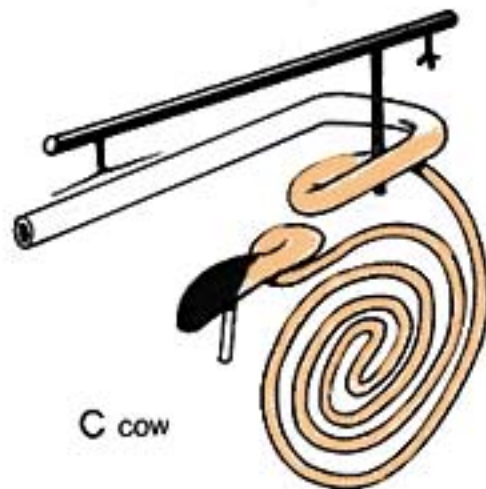
Ascending Colon Loop (right side view)



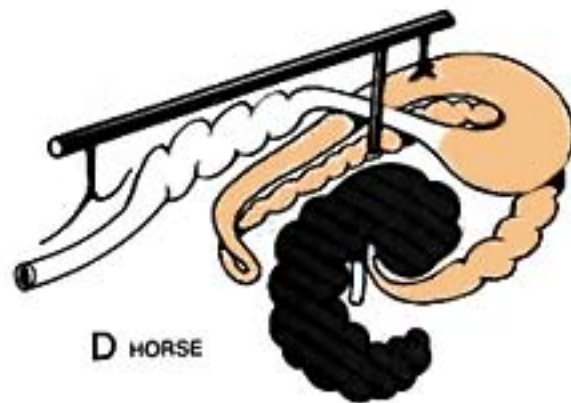
A DOG



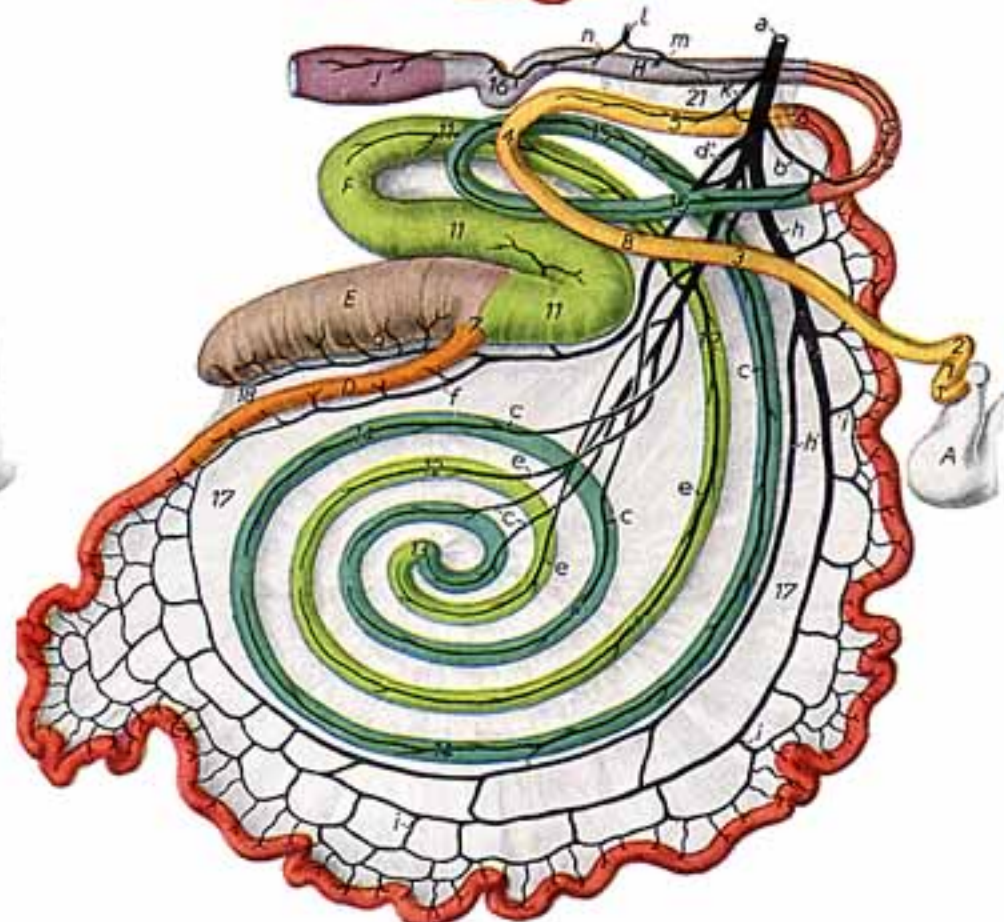
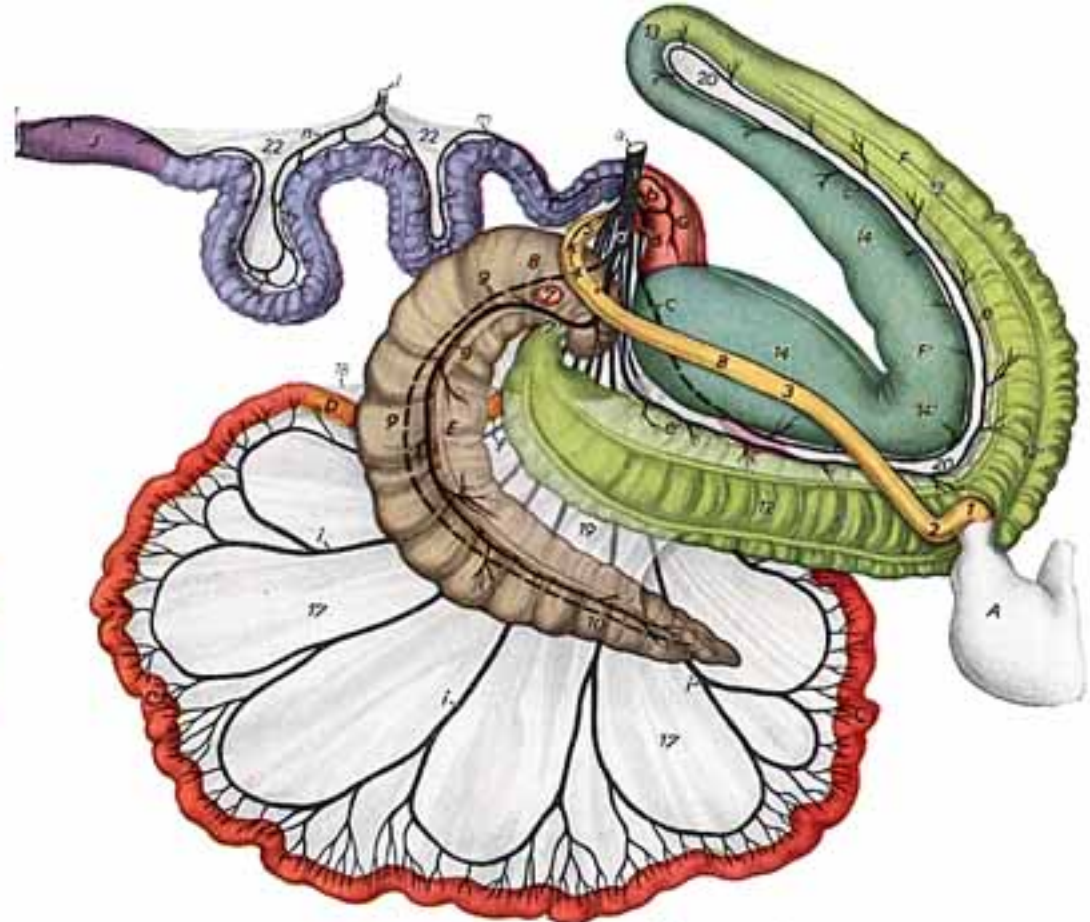
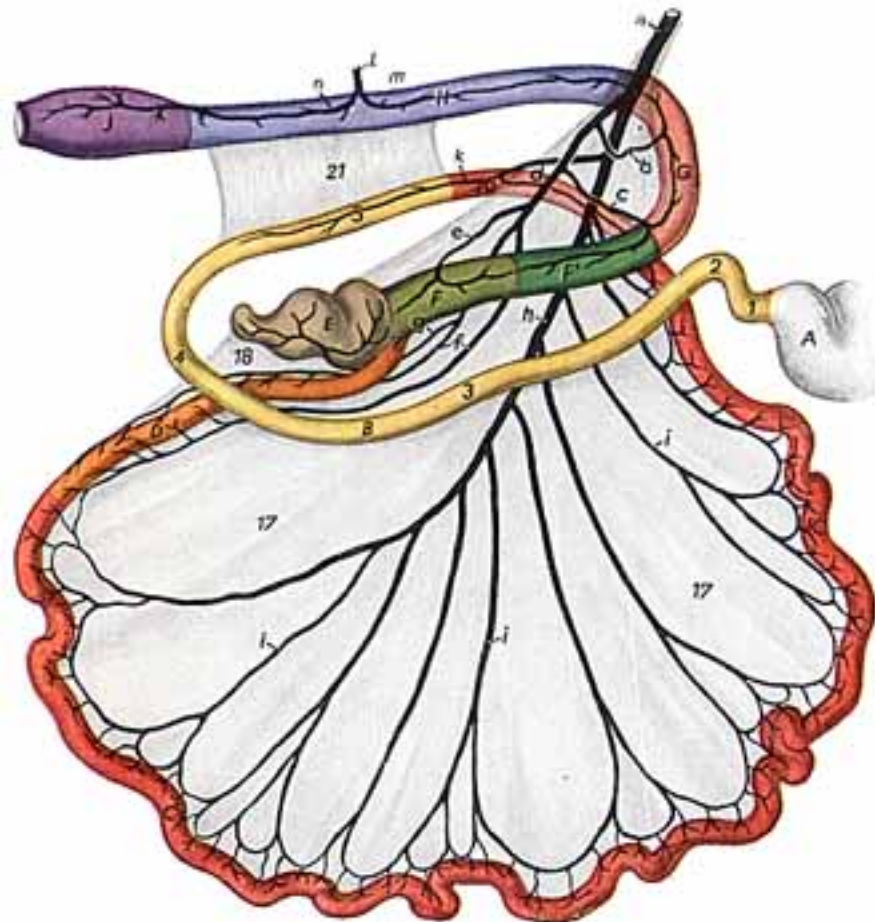
B PIG



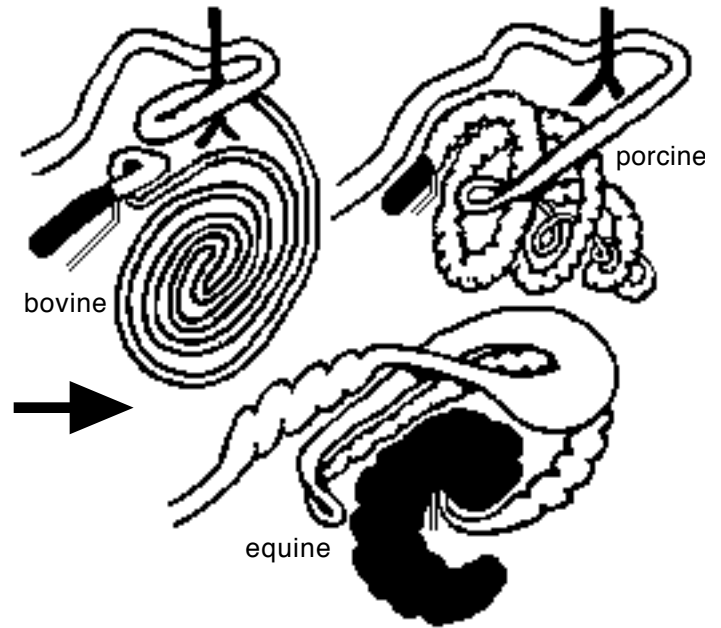
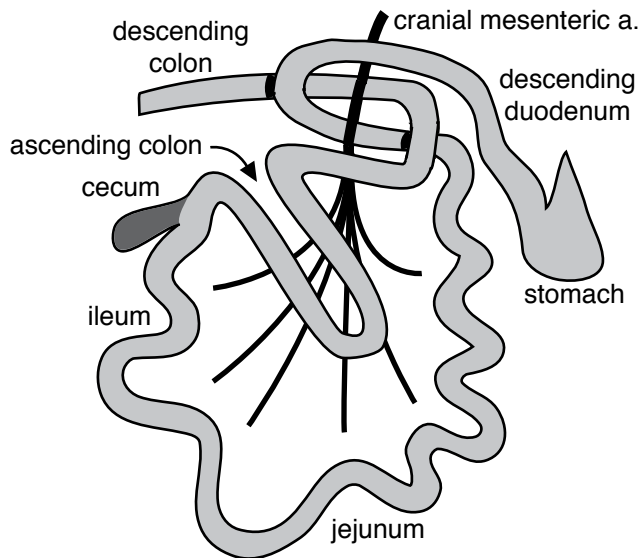
C COW



D HORSE



Ascending Colon Loop (right side view)

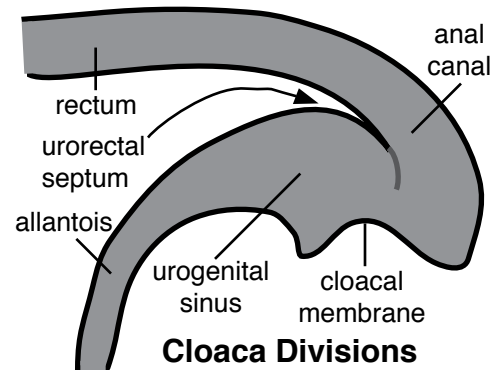


Cloaca...

The hindgut terminates in a cloaca, i.e., a chamber that communicates with the digestive, urinary and genital systems (the cloaca persists in adult birds, reptiles, & amphibians). The allantois evaginates from the hindgut at the cranial end of the cloaca. The caudal wall of the cloaca, which is formed by endoderm apposed to surface ectoderm, is designated *cloacal membrane*.

Rectum: The rectum is formed when a mesenchyme partition (urorectal septum) divides the cloaca into dorsal and ventral chambers. The dorsal chamber, which is continuous with the hindgut, becomes the rectum and most of the anal canal. The ventral chamber, the *urogenital sinus*, is continuous with the allantois.

The urorectal septum grows caudally and divides the cloacal membrane into an anal membrane dorsally and a urogenital membrane ventrally. The membranes subsequently disintegrate in normal development.

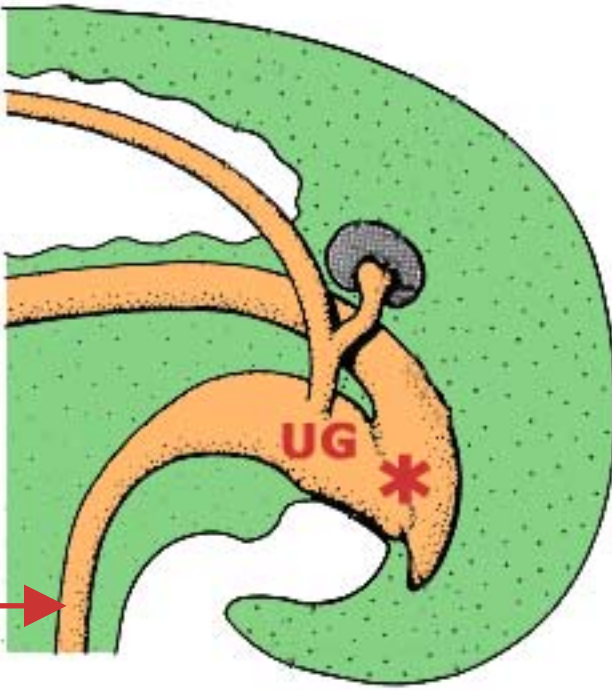


Anal canal: The cranial part of the anal canal (most of the canal) is formed with the rectum; this part of the anal canal is lined by a mucosal epithelium derived from endoderm. The caudal part of the anal canal (caudal to the adult anocutaneous line) is lined by stratified squamous epithelium. It forms as follows:

- tissue surrounding the anal membrane grows caudally creating a depression called the *proctodeum*; when the anal membrane degenerates, the proctodeum becomes incorporated into the anal canal (atresia ani or intact anal membrane is a congenital anomaly);
- in carnivores, lateral diverticula of proctodeum ectoderm become anal sacs.

NOTE: The urinary bladder develops from the cranial part of the urogenital sinus and the proximal end of the allantois.



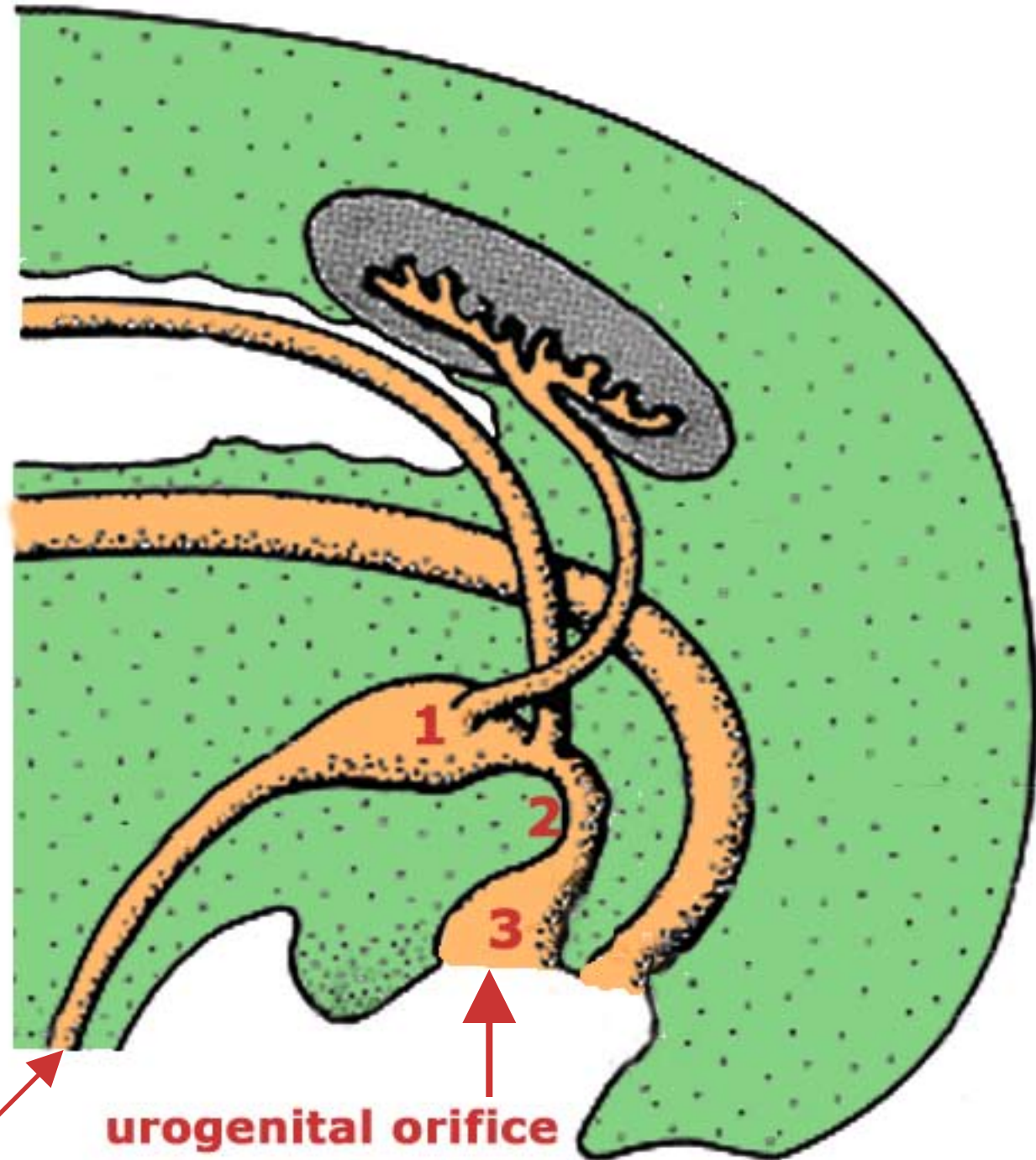


allantois →

Urogenital Sinus (UG) Male Female

- 1. urinary bladder
- 2. pelvic urethra
- 3. penile urethra

- urinary bladder
- urethra
- vestibule



urachus →

urogenital orifice

solitary
lymph
follicles

descending
colon

peritonerm

circular
muscle
of rectum

rectum

fat

anorectal
line

sphincter
ani:
internus
externus

anal
canal

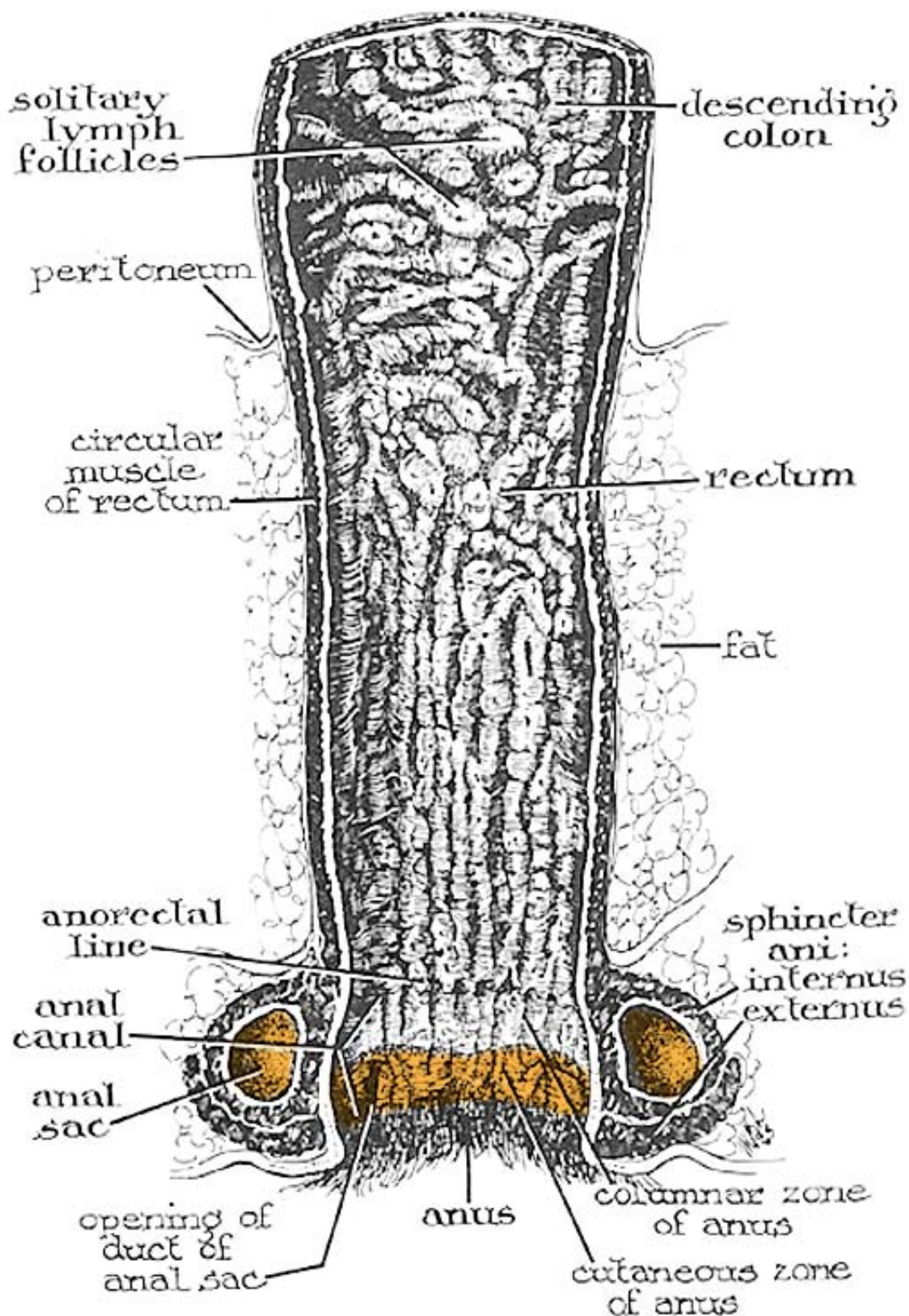
anal
sac

opening of
duct of
anal sac

anus

columnar zone
of anus

cutaneous zone
of anus



Liver...

The liver arises as an *hepatic diverticulum* of endoderm from the region of foregut that will become descending duodenum. The diverticulum gives rise to multiple branches that become: hepatic ducts, cystic duct and the pancreatic duct.

Continued growth and branching of hepatic duct primordia form the lobes of the liver. A gall bladder develops at the end of the cystic duct. The initial part of the hepatic diverticulum, from which the various branches arose, becomes the bile duct.

The hepatic diverticulum grows within ventral mesogastrium (lesser omentum). (The diverticulum temporarily penetrates the future diaphragm (septum transversum) which contributes connective tissue to the liver.)

The hepatic diverticulum originates ventrally but differential growth of the duodenal wall results in the bile duct entering the duodenum dorsally, with the pancreatic duct on the major duodenal papilla.

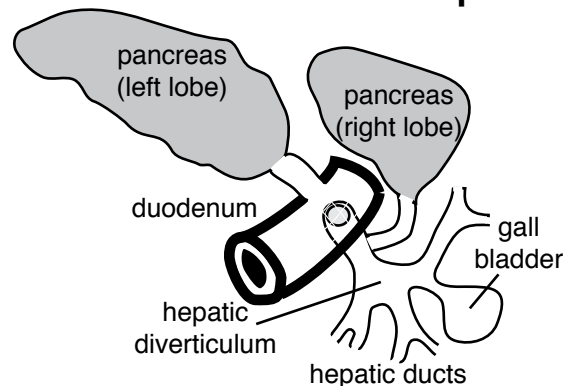
Pancreas...

The pancreas originates as two separate endoderm diverticula, each of which elongates, branches, and then forms acini in typical glandular fashion. One diverticulum arises ventrally as a bud of the hepatic diverticulum; it forms the pancreatic duct and right lobe of the pancreas. The other diverticulum arises dorsally from the duodenum (minor duodenal papilla) and forms the accessory pancreatic duct and the left lobe of the pancreas.

As the right and left lobes cross one another during development, they fuse to form the body of the pancreas; also, the duct systems anastomose to form a common system. The endocrine (islet) cells of the pancreas also develop from the endoderm of the diverticula.

NOTE: One of the two pancreatic ducts will be smaller than the other and may even disappear. Which one is destined to become smaller or absent depends on the species. In the dog, the accessory pancreatic duct is the larger one, but only about 20% of cats have an accessory pancreatic duct and the associated minor duodenal papilla.

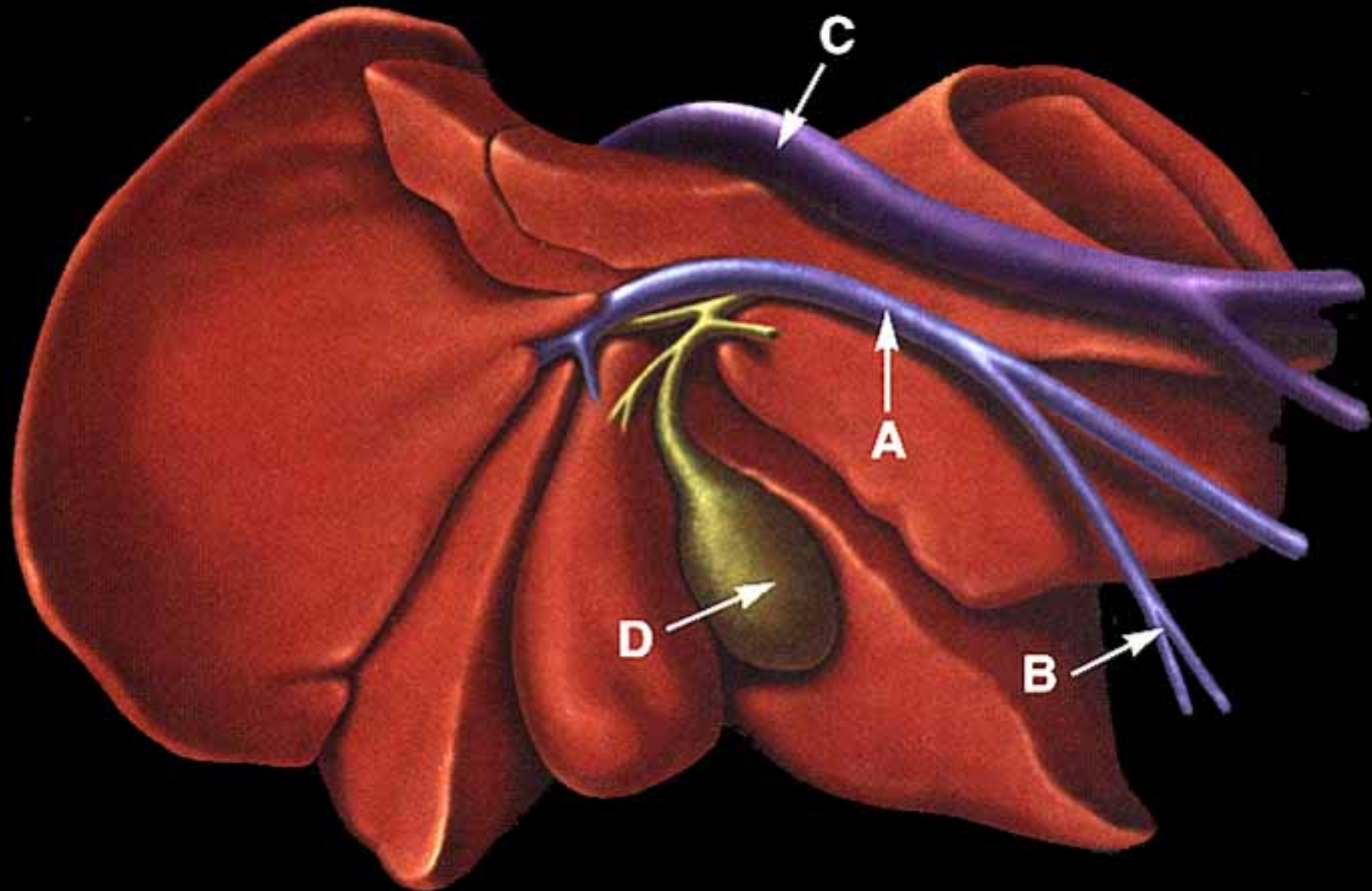
Pancreas & Liver Development



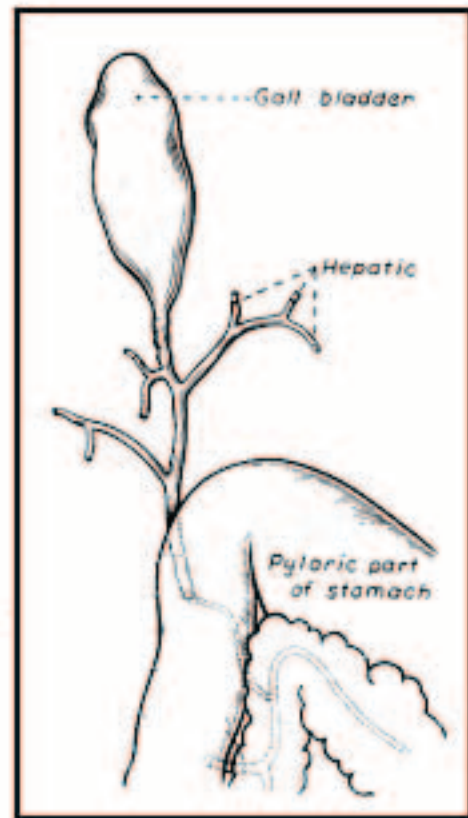
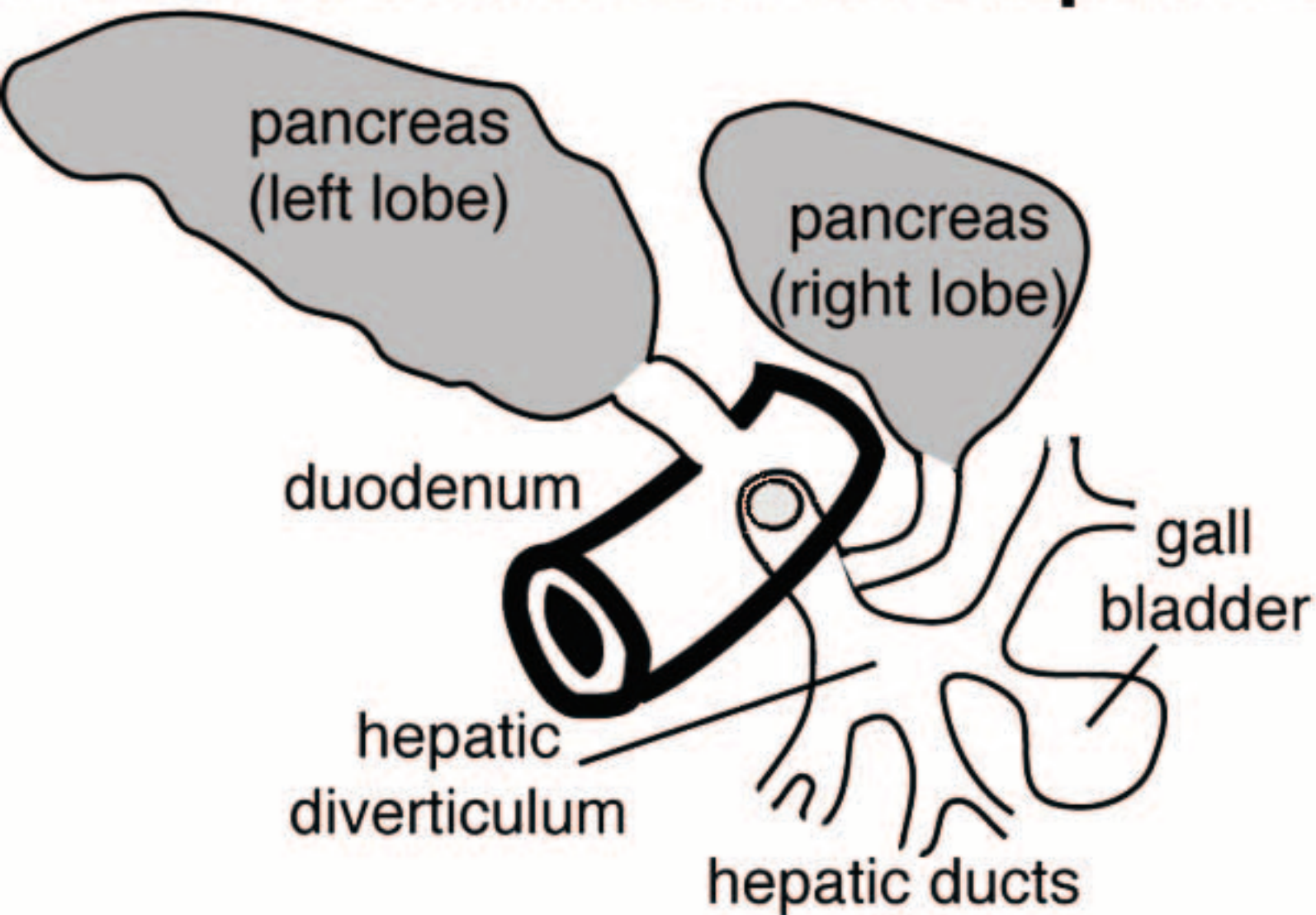
Avian...

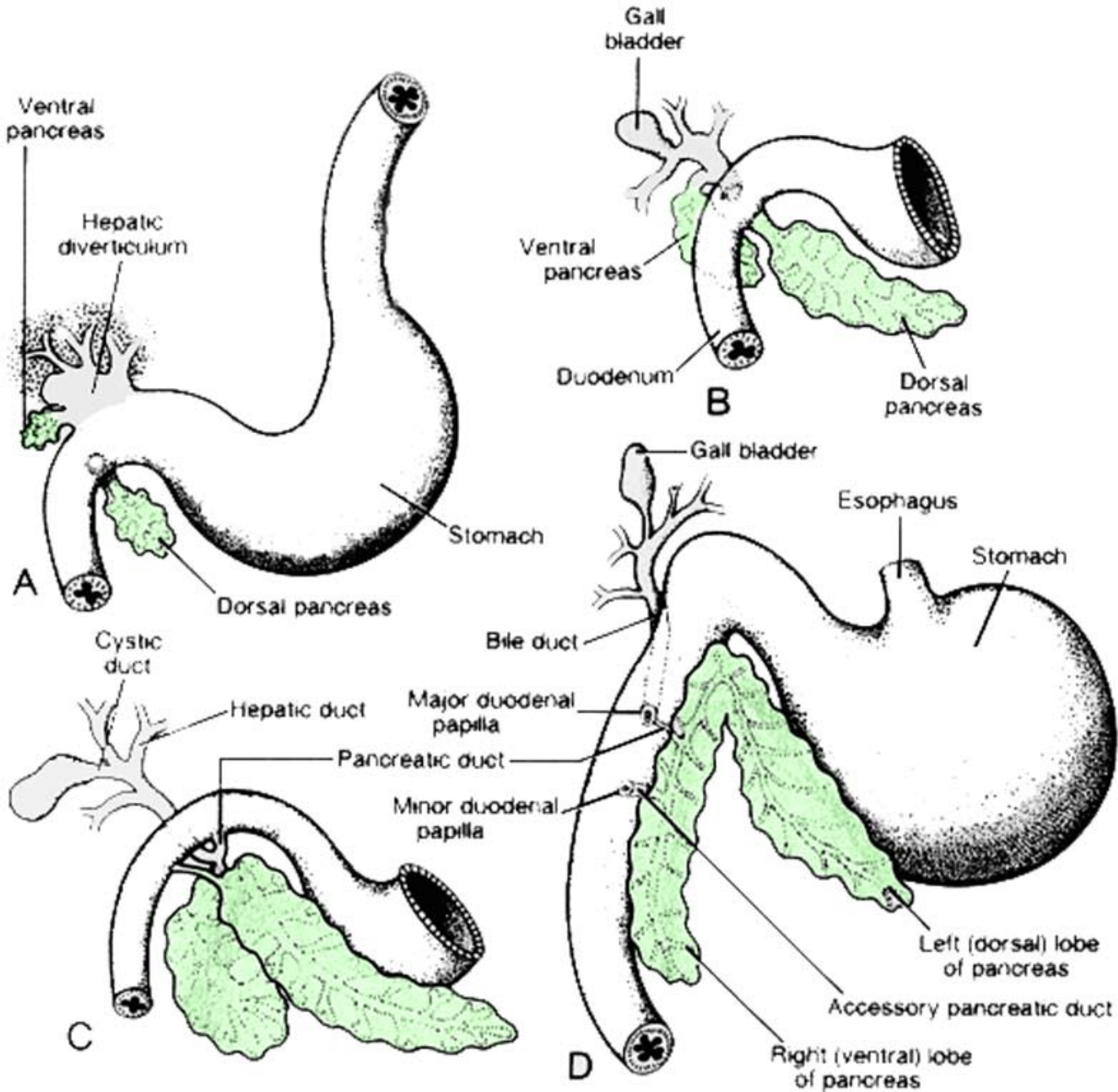
The avian digestive tract features:

- a crop, which develops as a diverticulum of the esophagus;
- a two-compartment stomach:
 - 1) proventriculus (glandular stomach) and
 - 2) ventriculus or gizzard (stratified squamous epithelium and heavy muscles for grinding);
- a pair of ceca;
- a cloaca which opens externally by means of a vent.



Pancreas & Liver Development





Mesenteries...

Mesenteries are formed by splanchnic mesoderm when the embryonic gut is created as the embryo assumes a tubular shape.

Splanchnic mesoderm is separated from somatic mesoderm by the embryonic coelom. Mesoderm lining the coelom transforms into serous membrane, making the coelom a serous cavity.

Caudal to the pharynx (head process), dorsal and ventral “mesenteries” of the esophagus persist as *mediastinum* in the thorax.

In the abdomen, a dorsal mesentery is continuous, but a ventral mesentery is absent caudal to the stomach and cranial to the cloaca.

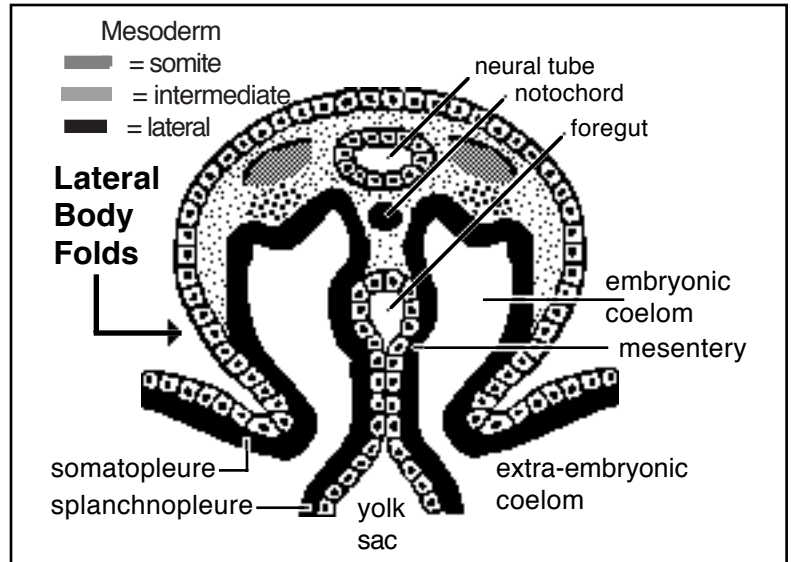
The dorsal mesentery becomes: greater omentum, mesoduodenum, mesentery (mesojejunum and mesoileum), mesocolon, and mesorectum.

The original dorsal mesogastrium elongates greatly as it forms *greater*

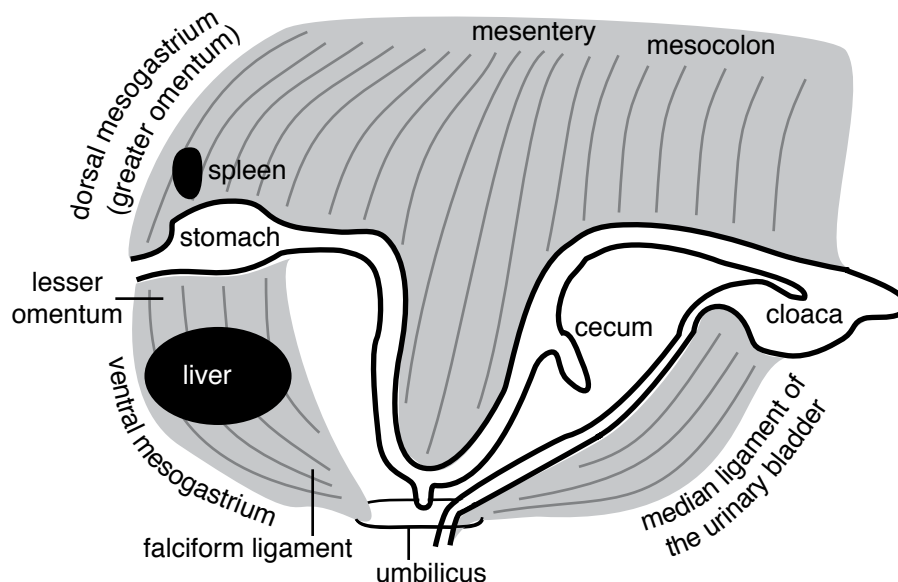
omentum. The left lobe of the pancreas develops within the dorsal portion of the greater omentum. The spleen develops within the greater omentum from blood vessels that accumulate in the vicinity of the greater curvature of the stomach.

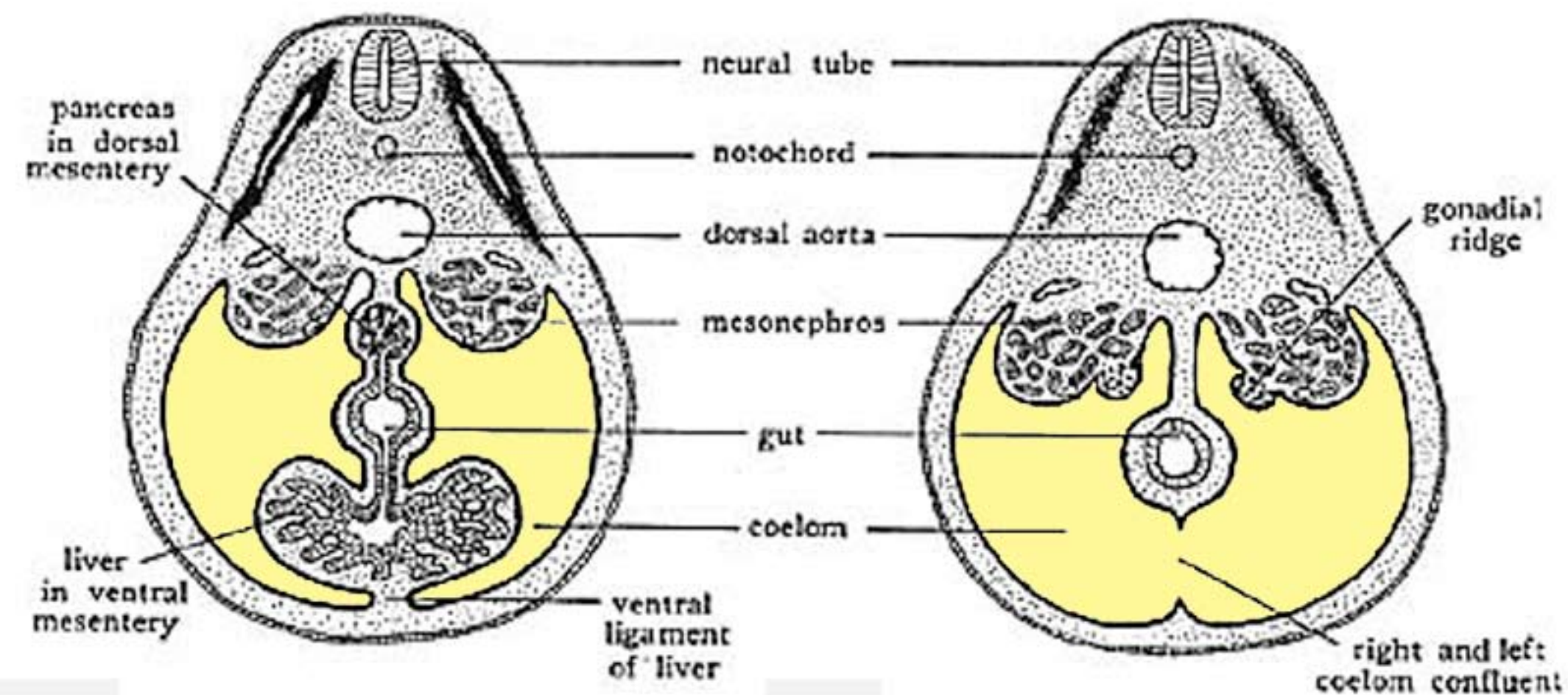
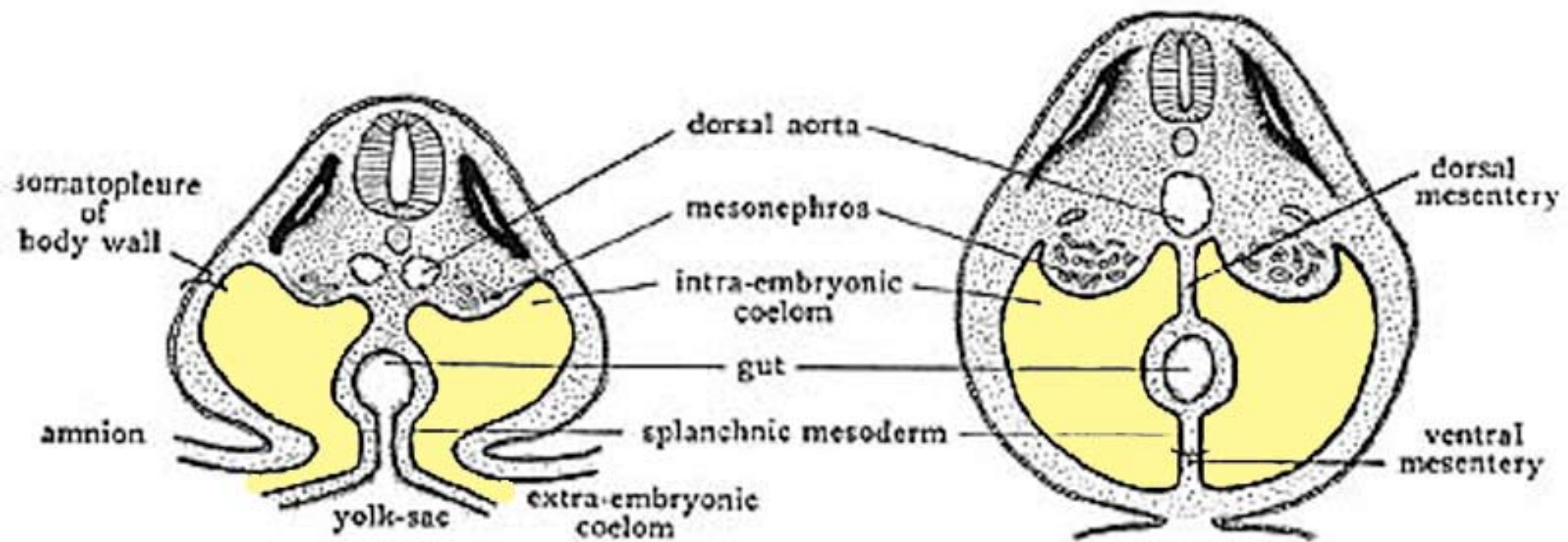
As the midgut elongates and rotates around the cranial mesenteric artery, portions of the mesojejunum and mesoileum come into contact near the dorsal body wall and fuse, forming the *root of the mesentery*. Parts of the mesoduodenum and mesocolon also fuse to the root the mesentery.

The ventral mesentery, in which the liver develops, becomes the *lesser omentum* and coronary and falciform ligaments of the liver. Caudally, ventral mesentery becomes *median ligament of the urinary bladder*.

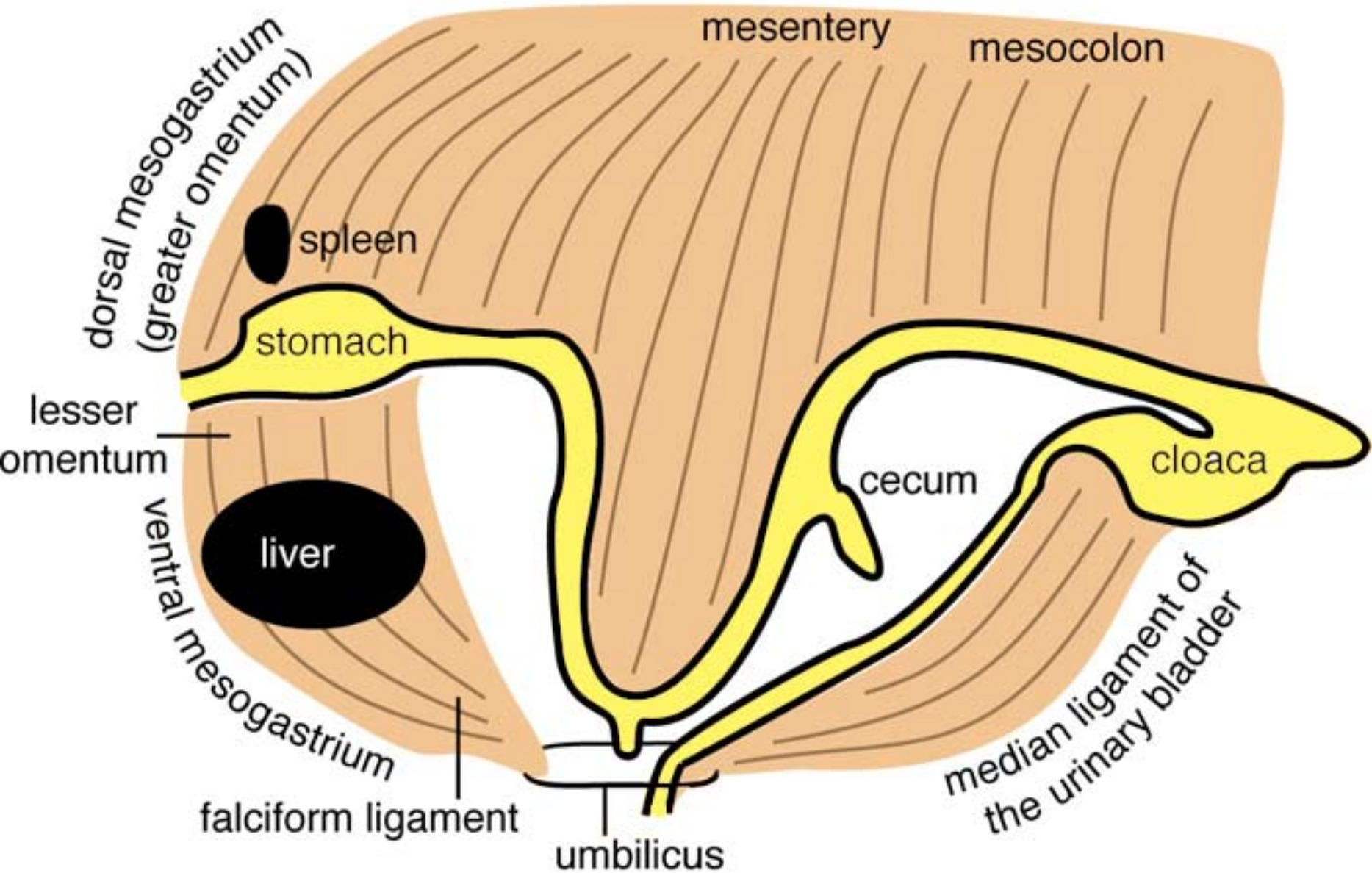


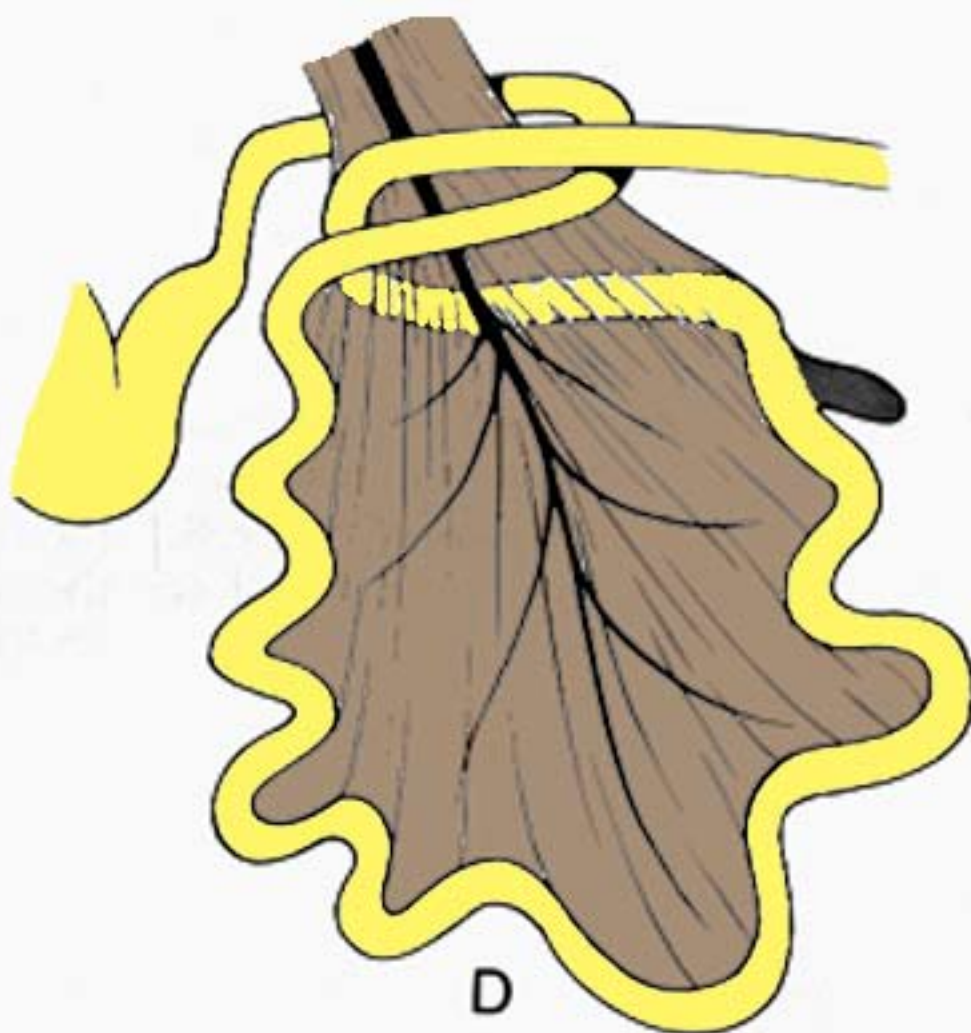
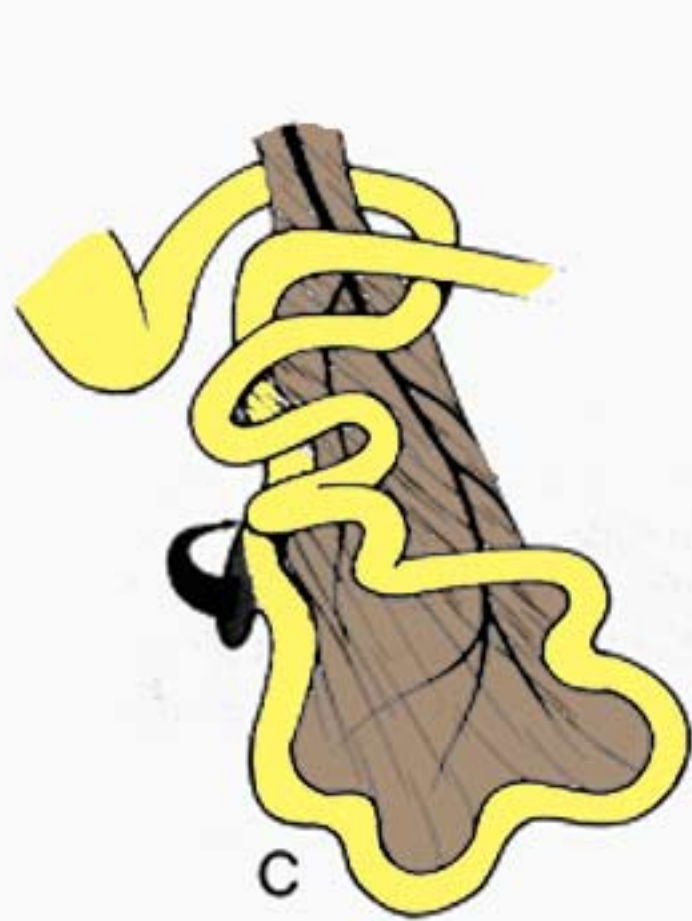
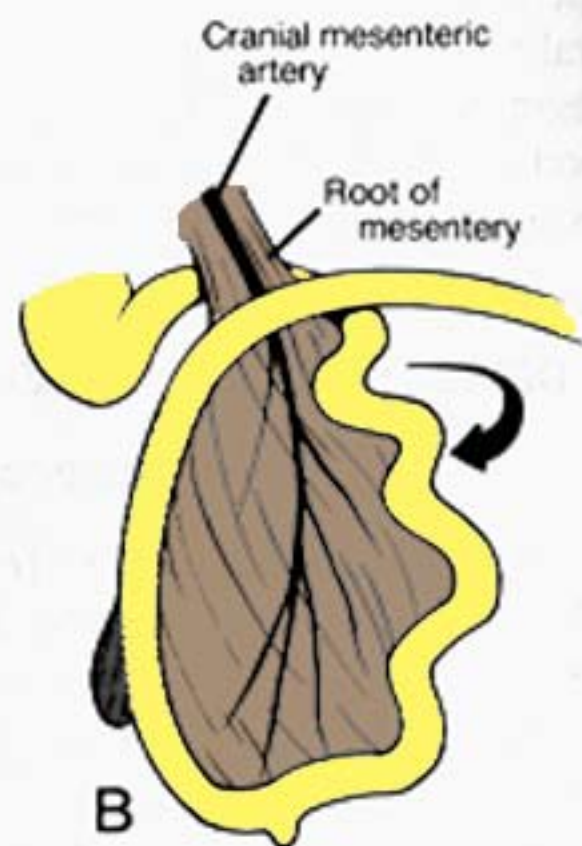
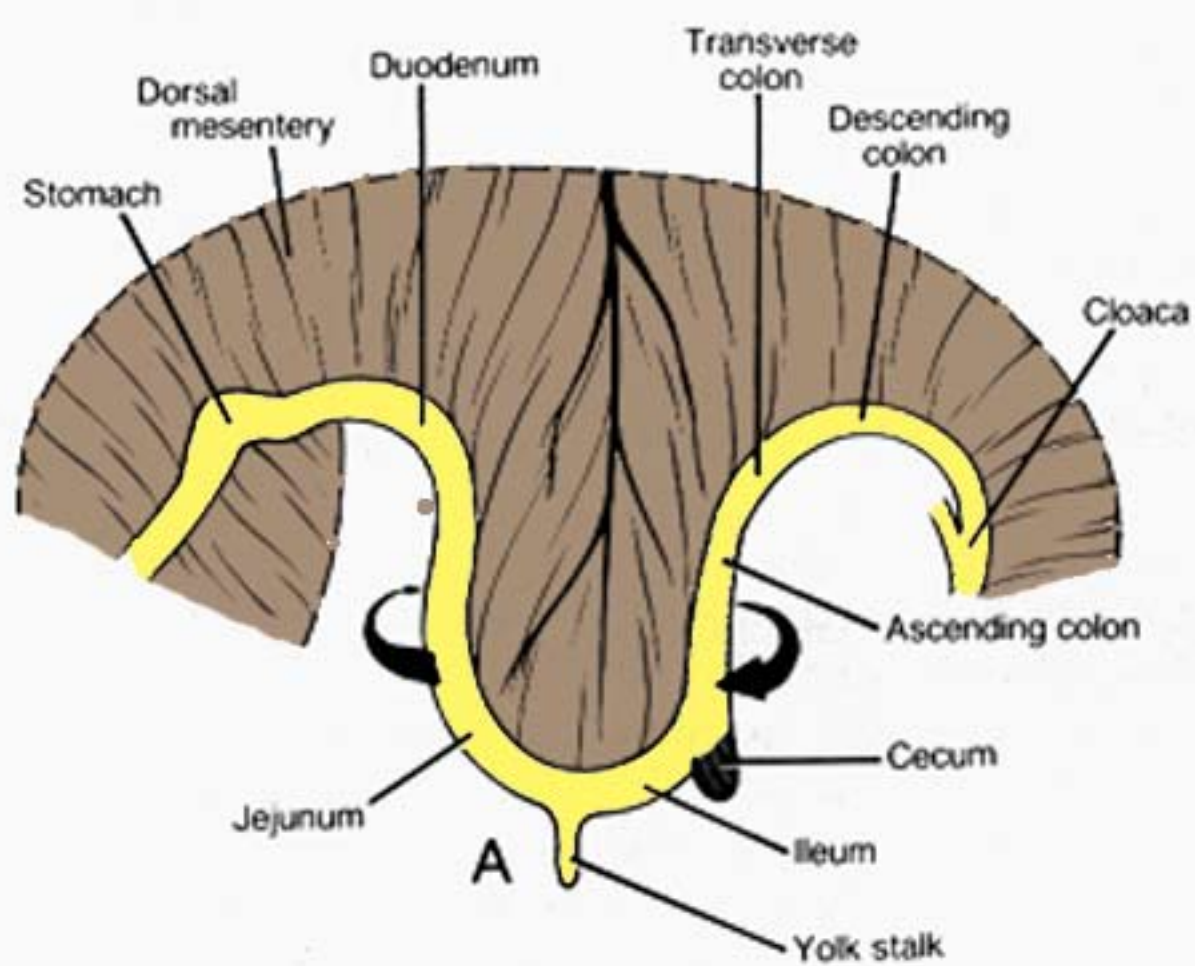
Mesenteries (lateral view)

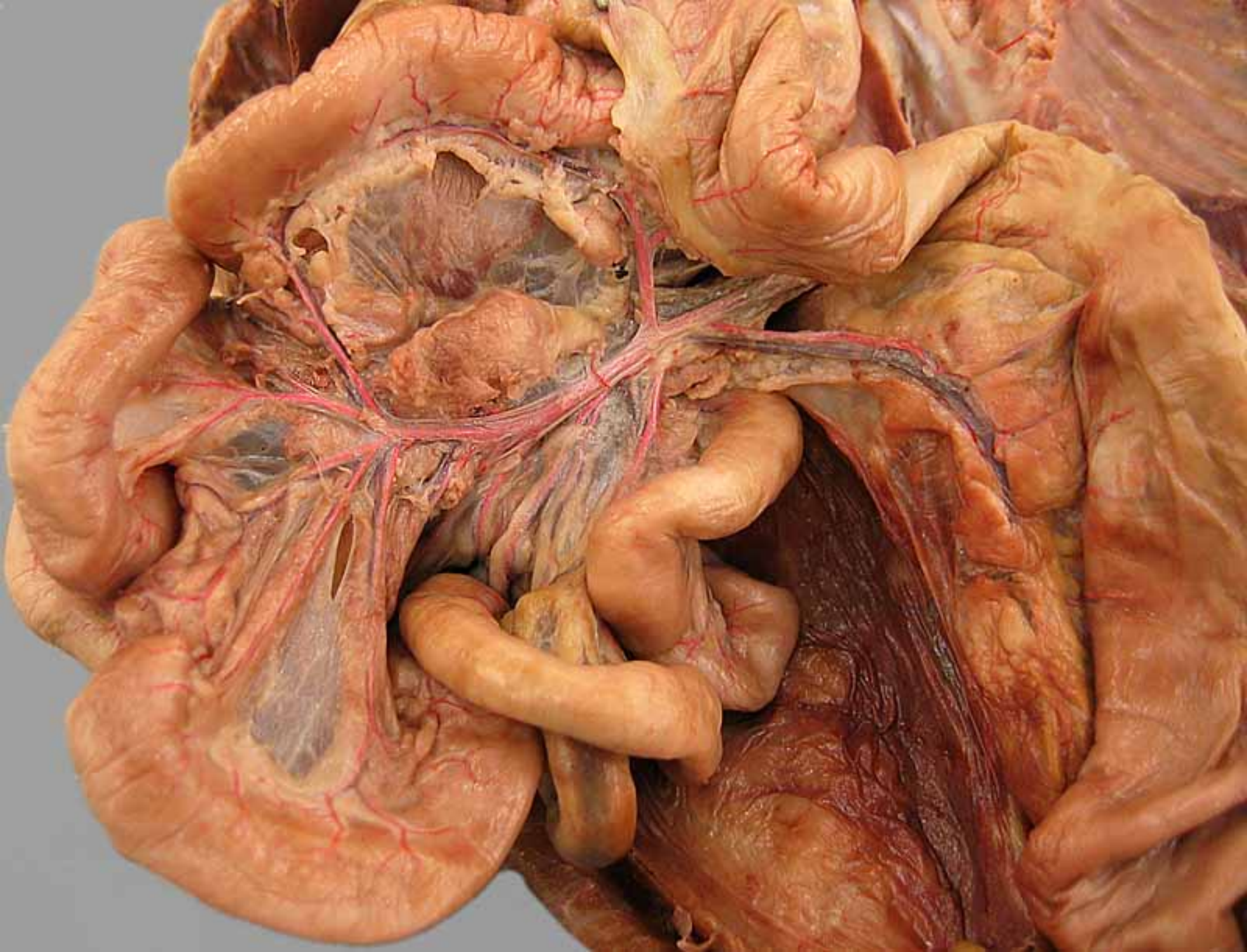


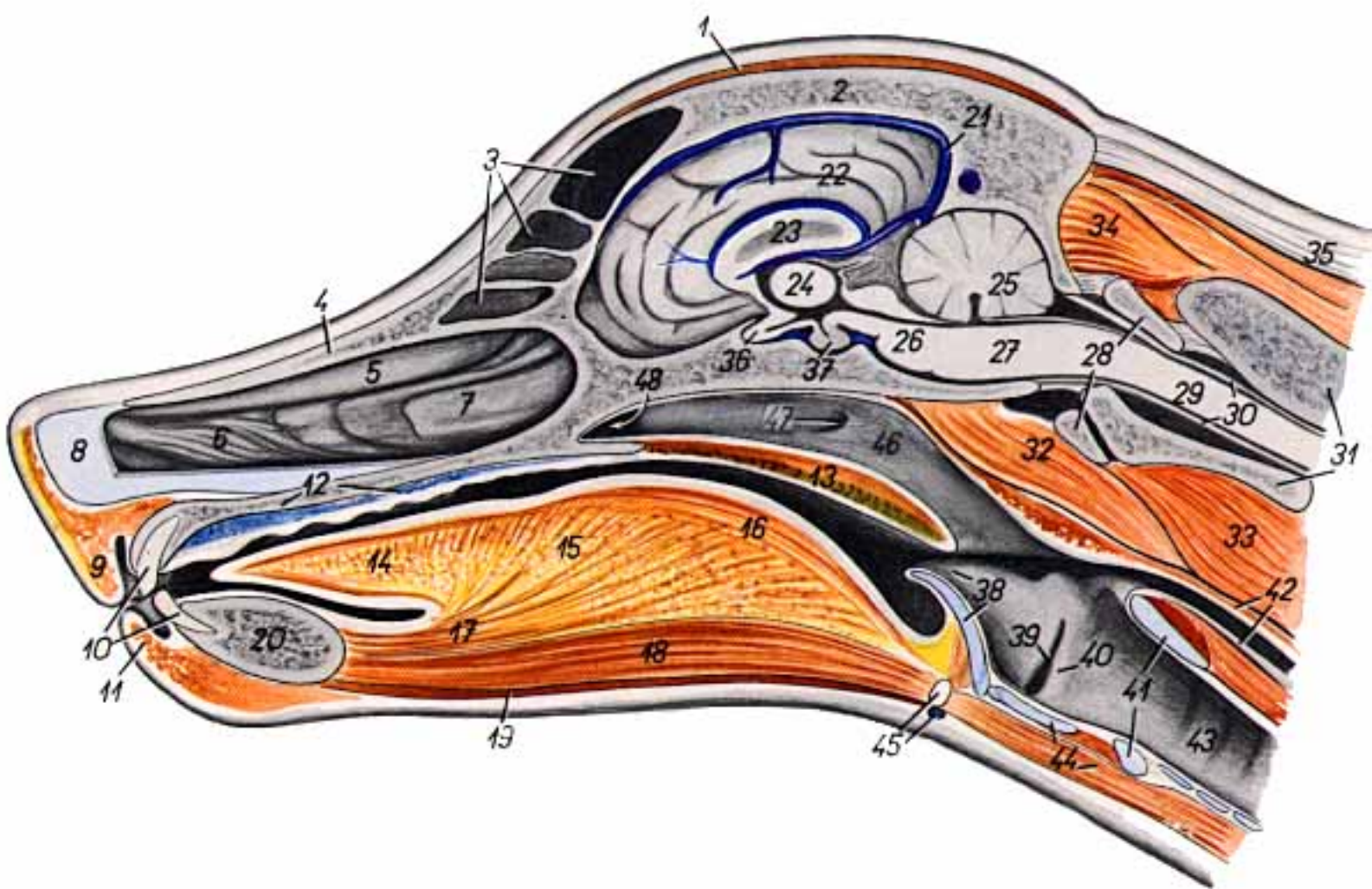


Mesenteries (lateral view)







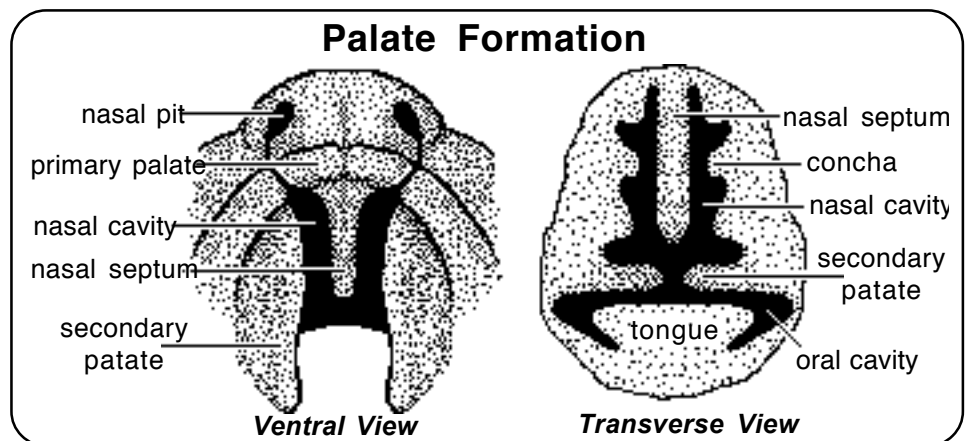


Respiratory System

The respiratory system consists of the nasal cavity, pharynx, larynx, trachea and lungs. The lining of the nasal cavity is derived from ectoderm; the lining of the rest of the respiratory system comes from endoderm.

Summary of Nasal Cavity Development: (details given later in Face Development lecture)

- initially, bilateral *nasal* (olfactory) *placodes* appear (the placodes are ectodermal thickenings at the ventral tip of the frontonasal prominence)
- placodes become *nasal pits* by outward growth of the surrounding *medial* and *lateral nasal processes* of the frontonasal prominence
- continued outgrowth of medial & lateral nasal processes elongates the nasal pits and transforms them into a *nasal cavity*
- right and left medial nasal processes fuse to form a *primary palate* (incisive bone & rostral upper lip) and a *nasal septum*; lateral nasal processes become nose cartilage and nasal & lacrimal bones
- formation of the *secondary palate* divides a common naso-oral space into three separated cavities (right & left nasal cavities and the oral cavity); also, the secondary palate divides the pharynx into three compartments (nasopharynx, oropharynx, & laryngopharynx)



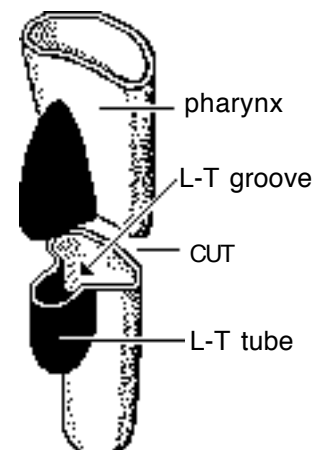
- *conchae* (scrolls of thin bone covered by mucosa) arise as cartilaginous ridges from bones of the nasal cavity wall
- *paranasal sinuses* (diverticula of the nasal cavity) develop postnatally.

Larynx, Trachea and Lungs:

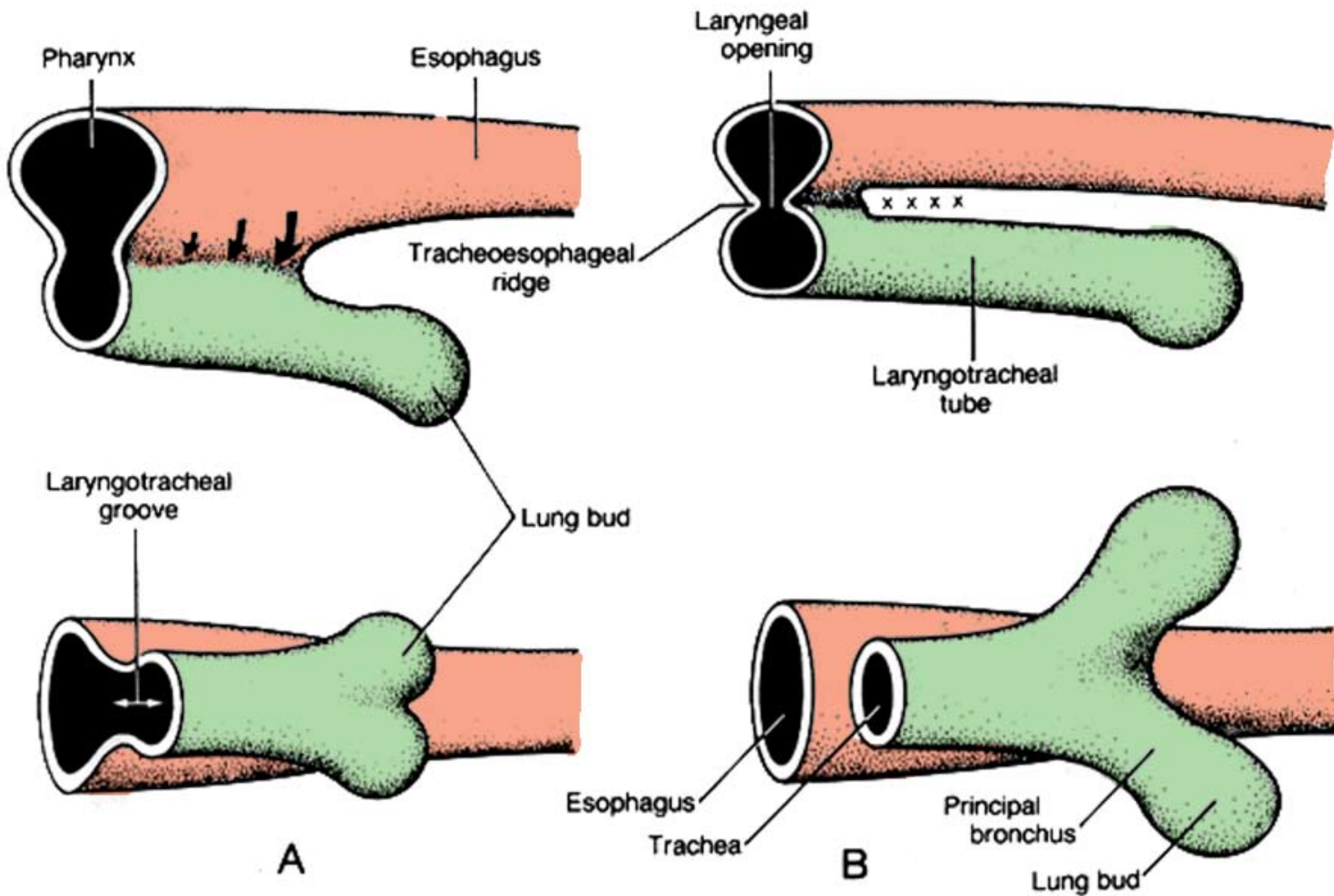
These respiratory structures originate as an evagination of endoderm along the floor of the pharynx. The evagination is designated the *laryngotracheal groove*.

From lateral walls of the laryngotracheal groove, ridges grow medially, and fuse along the midline, establishing a tracheoesophageal septum. The septum separates a *laryngotracheal tube* (future trachea & lung buds) from the esophagus.

The larynx develops rostrally, where the lumen of the groove retains communication with the pharynx.



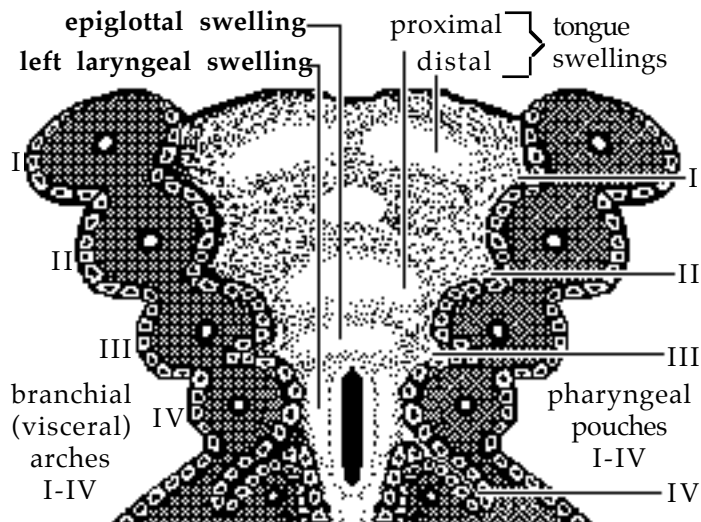
Laryngo-Tracheal Groove (ventral view)



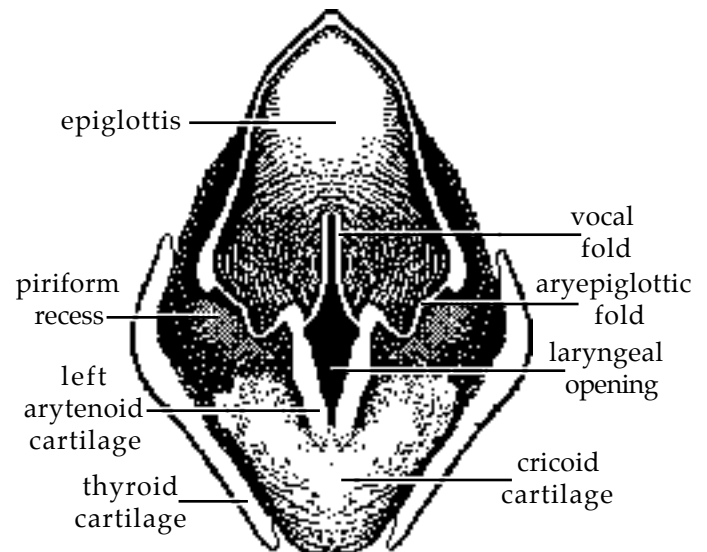
Larynx:

The wall of the larynx originates from growth of bilateral laryngeal swellings (future arytenoid, thyroid, & cricoid cartilages) and a rostral epiglottal swelling. The swellings border the persistent laryngeal opening (between laryngotracheal groove and the pharynx). A diverticulum of the lateral laryngeal wall produces a lateral ventricle & vocal fold (except in cats & cattle).

Pharyngeal arch splanchnic mesoderm forms laryngeal swellings and cartilages. Muscles develop from somite myotomes that migrate into pharyngeal arches: IV (cricothyroideus m. innervated by the vagus n. cranial branch) & VI (other muscles innervated by the vagal recurrent laryngeal n.)



Dorsal View of Floor of Pharynx (roof removed)



Dorsal View of Larynx

Trachea and bronchi:

The *laryngotracheal tube* grows caudally into splanchnic mesoderm located ventral to the pharynx. The mesoderm contributes cartilage and connective tissue and endoderm contributes respiratory epithelium to the developing trachea. Tracheal elongation shifts bronchi caudally into the thorax.

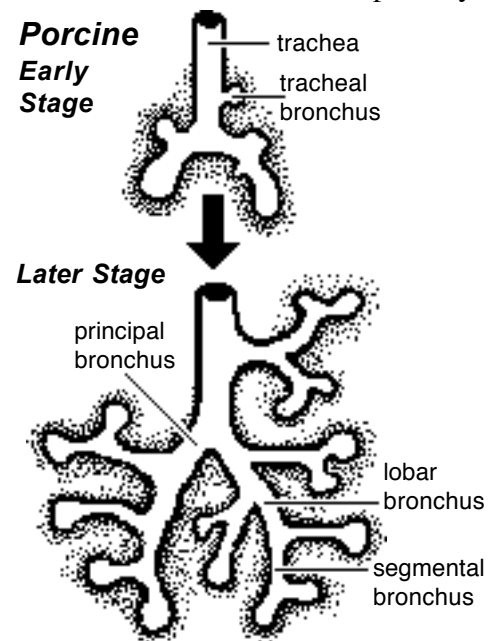
The blind, caudal end of the tube develops bi-lobed bronchial buds which grows to form the future *principal bronchi*.

Outgrowths of each principal bronchus form future lobar bronchi, each of which gives rise to outgrowths that become future segmental bronchi, each of which gives rise to more than a dozen additional bronchial branches. The smallest branches are bronchioles. They give rise to lung terminal sacs and alveoli.

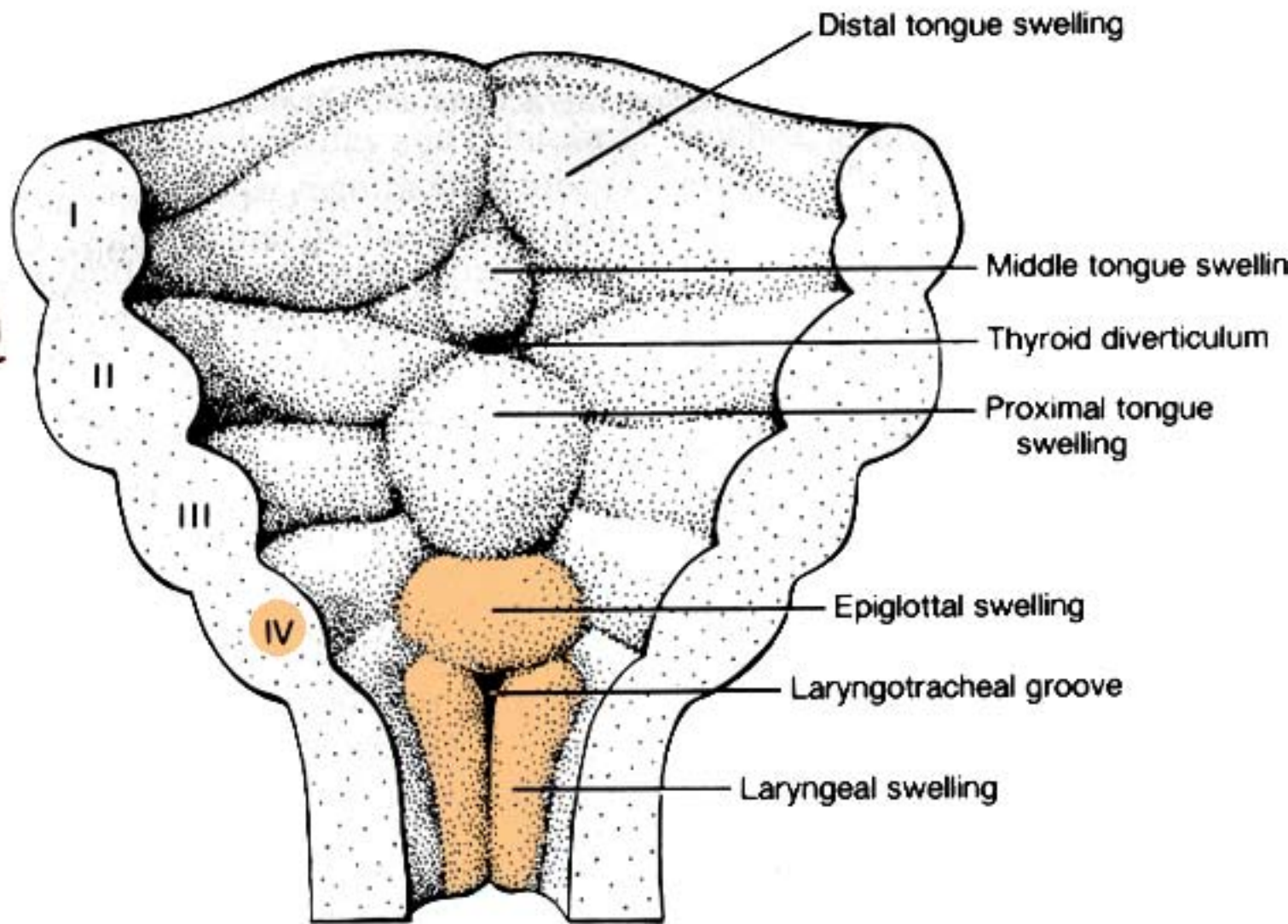
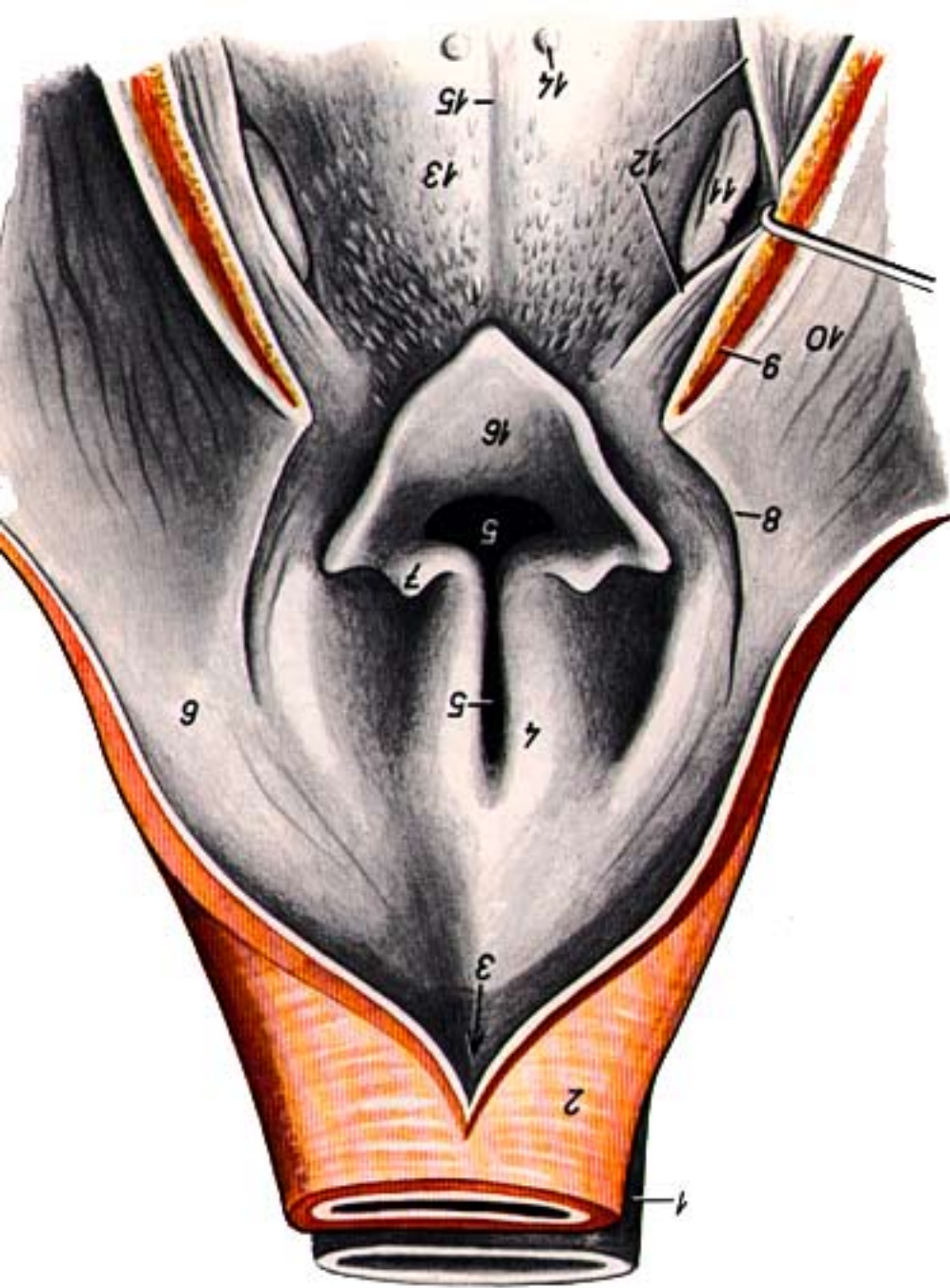
The bronchial branchings continue to occur throughout the fetal period and into the postnatal period.

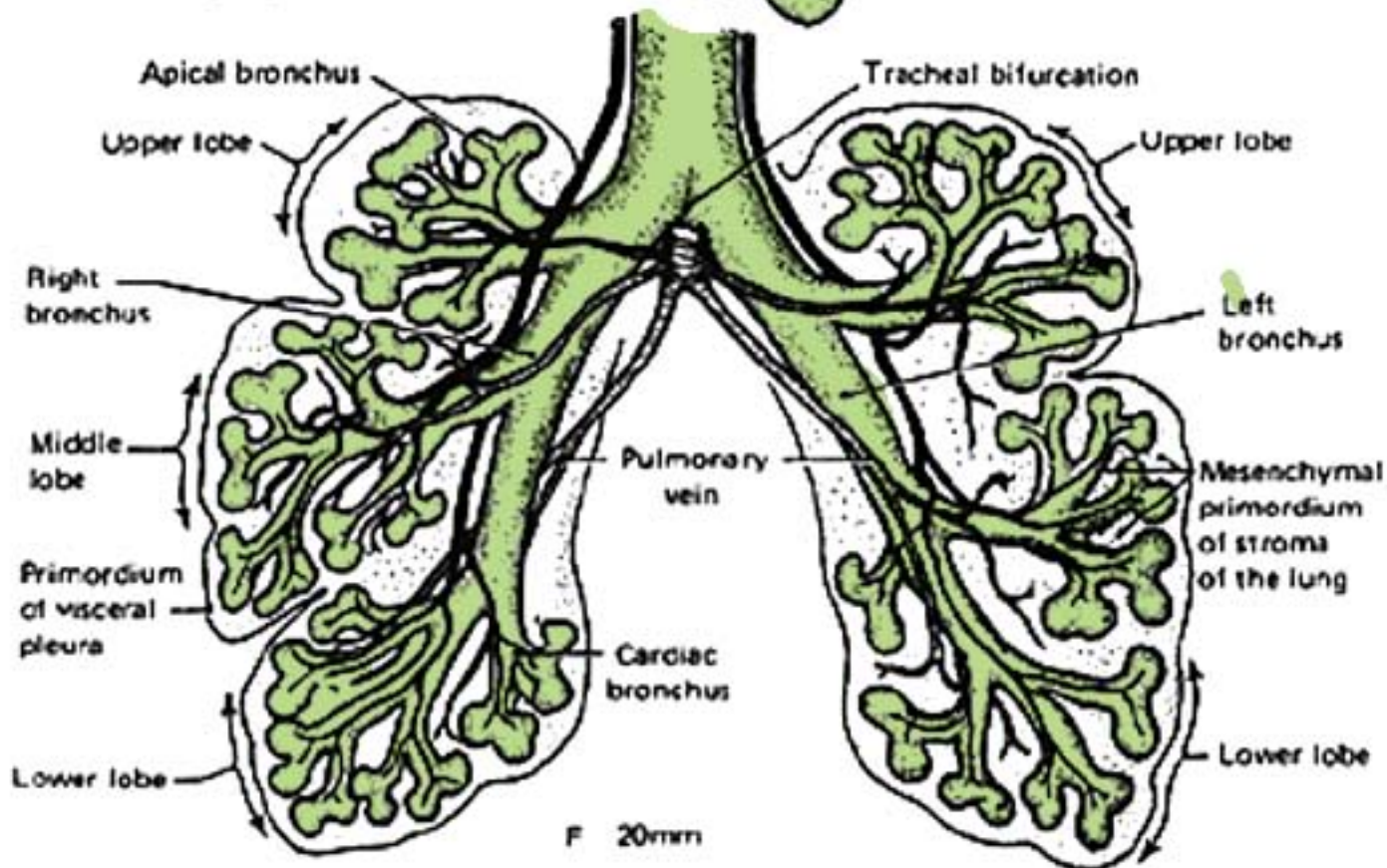
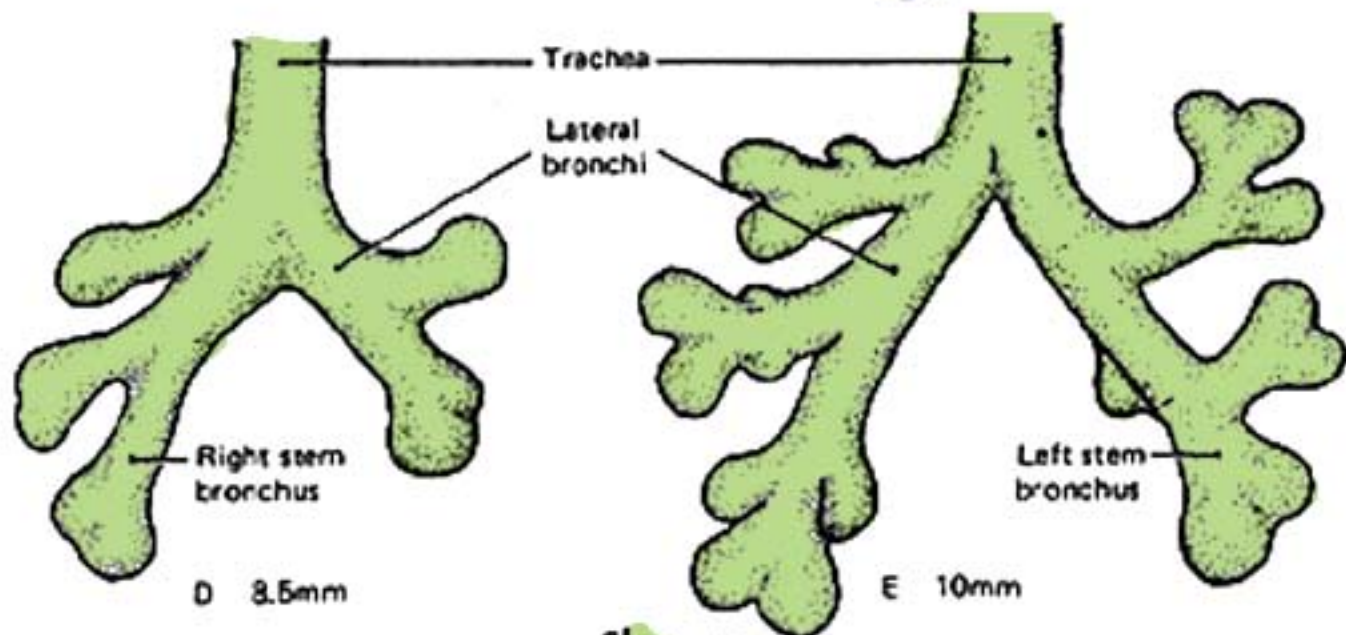
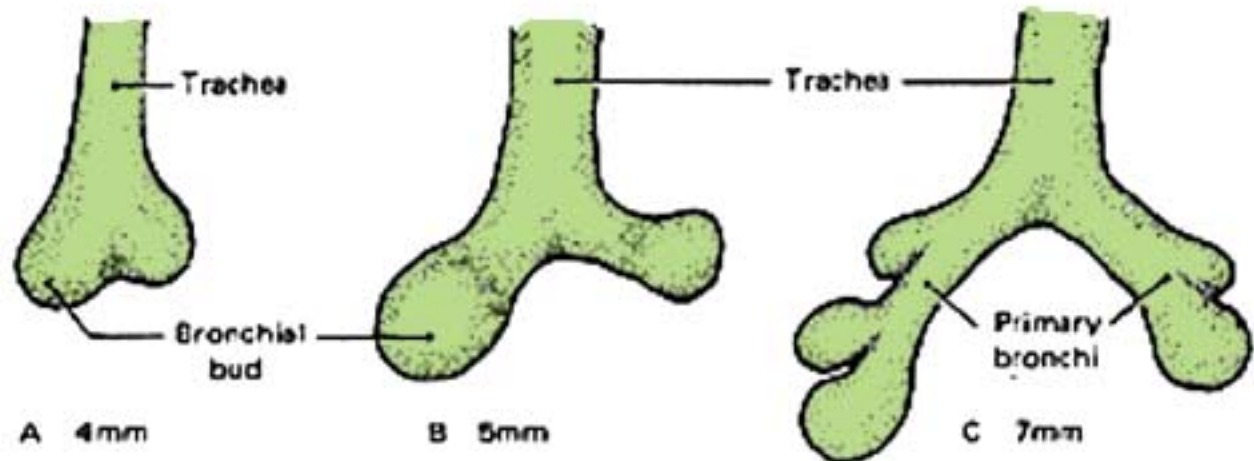
NOTE: Generally in domestic mammals, the right principal bronchus divides into four lobar bronchi (to cranial, middle, caudal & accessory lobes), while the left gives rise to two lobar bronchi (to cranial & caudal lobes).

There are right side exceptions: the horse lacks a middle lobe; (humans lack an accessory lobe;) in ruminants and swine the right cranial lobe is supplied by a tracheal bronchus.



Bronchial Development
(Dorsal View)





Lungs:

Continued branching of the bronchial tree results in lung tissue occupying more and more of the pleural cavity, coated by visceral pleura. The endoderm-lined bronchial tree grows into splanchnic mesoderm which forms the cartilage, fascia, smooth muscle, and vessels of the lung.

Initially, bronchiole-lung branches are **solid cores** of cells that grow into splanchnic mesoderm (growth is like exocrine gland growth into mesoderm). Eventually, terminal branches become hollow, dilated, and sac-like with endoderm becomes a thin epithelium (terminal sacs). Alveoli are created by the formation of septae that partition the terminal sacs.

Some endodermal alveolar cells become cuboidal rather than flat and produce a phospholipid surfactant that reduces surface tension and thus facilitates alveolar expansion (as opposed to alveolar collapse). Fetal lungs contain fluid that facilitates the breathing movements that take place *in utero* to prepare for postnatal respiration. At birth, lung fluid drains or is absorbed as air is breathed.

NOTE: Species differ in degree of lung maturity at birth. Also, within a single lung, distal regions are less mature than proximal ones. Formation of new alveoli occurs post-natally to a considerable extent in all mammals. Subsequently, lung growth is due to hypertrophy (increased size) of alveoli and air passageways.

Alveolar Formation

