DEVELOPMENT OF DIGESTIVE TRACT

- Development of the primitive digestive tract commences with the cranial, caudal and lateral foldings of the embryonic disc and the incorporation of the dorsal portion of the primitive yolk sac into the embryo.
- The endodermally-lined cranial portion of the tract formed within the head fold is termed the foregut, the part formed within the caudal fold is referred to as the hindgut, while the segment of embryonic endoderm between the foregut and hindgut, which is continuous with the yolk sac, is called the midgut.
- Progressive folding of the embryo constricts the wide connection between the midgut and yolk sac until only a narrow connection, the vitelline duct, remains between these two structures. The blind end of the foregut is apposed to an ectodermal depression in the developing head region, the stomodeum, which later forms the oral cavity.

- A similar ectodermal depression, in contact with the blind end of the hindgut, the proctodeum, later forms the anus.
- The ecto-endodermal membrane, which separates the stomodeum from the foregut, is called the oropharyngeal membrane; the structure between the hindgut and proctodeum is termed the cloacal membrane.
- As development progresses, both these membranes regress and the oral cavity becomes continuous with the foregut and the hindgut opens to the exterior.
- Two major abdominal organs, the liver and pancreas, arise as outgrowths from the distal region of the foregut.

- The primitive alimentary tract is composed of an inner endodermal lining and an outer layer of splanchnic mesoderm.
- The epithelium of the digestive tract and its associated glands are derivatives of endoderm while the splanchnic mesoderm gives rise to the smooth muscle and connective tissue of the tract.
- Subsequently, these tissues become organised into four basic histological layers: mucosa, submucosa, muscularis externa and serosa or adventitia.
- As the length of the alimentary tract increases, development of the muscularis externa proceeds along the cranial–caudal axis with the inner circular layer appearing first, followed by the outer longitudinal layer.

- Wide variations, evident in the structure and function of digestive systems of animals, reflect their evolutionary development.

- These differences apply particularly to structures associated with the prehension, mastication and digestion of food.

- Carnivores have short, simple gastrointestinal tracts; in contrast, herbivores usually have long, voluminous, compartmentalised digestive tracts.

ESOPHAGUS

- The oesophagus, which at first is a short tube, extends from the tracheal groove to the fusiform dilation of the foregut, the primordial stomach. In association with the elongation of the cervical region of the embryo, the oesophagus increases in length.
- Along its length, the endoderm of the oesophagus is surrounded by somatic mesoderm of the head, which develops into striated muscle.
- Species variation is evident in the extent to which the oesophagus is invested with skeletal muscle.
- In ruminants, the muscular component consists entirely of striated muscle.
- With the exception of a short terminal portion where the inner circular muscle layer is composed of smooth muscle, oesophageal muscle in carnivores is skeletal.

- In the porcine oesophagus, a short region near the stomach is composed of smooth muscle, while in horses and cats the smooth muscle extends over the caudal third of the oesophagus.
- In the early stages of development, oesophageal epithelium is columnar. Later, this epithelium becomes stratified and squamous in all species, with keratinisation evident in herbivores.
- Oesophageal glands, which develop from the epithelium, are located in the submucosal layer.
- In domestic animals, these branched, tubulo-alveolar mucous glands vary in their distribution along the length of the oesophagus.

STOMACH

- The stomach, which can be recognised early in embryological development as a fusiform dilation of the caudal part of the foregut, is attached to the dorsal abdominal wall by the dorsal mesogastrium and to the ventral wall by the ventral mesogastrium.
- Because the dorsal region of the stomach grows at a greater rate than the ventral region, this organ changes morphologically, resulting in the formation of a dorsal greater curvature and a ventral lesser curvature.
- Further growth at the cranial aspect of the greater curvature gives rise to the primordium of the fundus of the simple stomach.

STOMACH

- During its early development, the stomach undergoes two rotations.
- In the first rotation, the organ moves through an angle of 90° to the left about a cranial–caudal axis, which results in the former left side assuming a ventral position and the former right side a dorsal position.
- At this stage of development, the stomach is a C-shaped sac, flattened dorso-ventrally with greater and lesser curvatures.

STOMACH

- Subsequent rotation of the stomach through a 45° angle in an anti-clockwise direction about a dorsal– ventral axis results in its caudal portion occupying a position to the right of the median plane.
- Consequently, the greater curvature of the stomach is directed to the left and caudally within the abdomen.
- The anatomical region of the stomach into which the oesophagus opens is referred to as the cardia.
- The portion which lies above the level of the cardia is called the fundus.
- The large middle portion of the stomach is termed the body and the most distal area is referred to as the pylorus.

Bovine stomach

- The gastric primordium of a 30-day-old bovine embryo is a spindle-shaped structure similar to the gastric primordium of animals with simple stomachs at a comparable stage of development.
- This primordial structure has a dorsal greater and ventral lesser curvature and undergoes rotation to the left in a manner similar to that which occurs in simple-stomached animals.
- The fundic region of the gastric primordium extends cranially and to the left of the median plane.
- By the 34th day, this cranial expansion, which represents the primordium of the rumen and reticulum, is prominent.

Bovine stomach

- An evagination develops along the lesser curvature which forms the embryonic omasum.
- Caudal to the embryonic omasum, the gastric primordium curves to the right and demarcates the future abomasum.
- Differential growth of the rumino-reticular primordium results in enlargement both in a cranial direction and to the left of the median plane.
- At this stage, the ruminoreticular primordium occupies a position between the developing liver and the left mesonephros.

- By about the 37th day, the rumino-reticular groove, which marks the boundary between the rumen and reticulum, is evident on the ventral surface of the rumino-reticular primordium.
- As the embryonic rumen continues to expand, cranial and caudal grooves partially divide it into two compartments.
- The primordia of the four compartments of the ruminant stomach, namely the rumen, reticulum, omasum and abomasum, are clearly demarcated by the 40th day of development.
- At this stage, each of these four compartments is lined by columnar epithelium.

- <u>Changes in the compartments of the bovine stomach from birth to maturity</u>

- Postnatal development of the gastric compartments in cattle is induced in part by dietary changes.
- For the first weeks of life, a calf ’s diet consists mainly of liquids which bypass the rumen, reticulum and omasum and enter the abomasum by way of the reticular groove.
- The rumen, reticulum and omasum have no role in digestion during this period.
- With the dietary change from liquids to solids, these three compartments become functional and increase in size. Relatively, the capacity of the abomasum changes minimally.

- <u>Changes in the compartments of the bovine stomach from birth to maturity</u>

- Thus, in the newborn calf, the abomasum is about twice the size of the combined rumen and reticulum, while at three months of age the abomasum is only half the size of these combined compartments.
- At four months, the rumen and reticulum are four times larger than the combined omasum and abomasum.
- From about 18 months, the rumen accounts for approximately 80% of the total capacity of the four compartments, the reticulum 5%, and the omasum and abomasum can each account for 7–8% of the capacity.

LIVER

- The liver develops as a hollow ventral diverticulum from the caudal region of the foregut.
- The diverticulum divides into cranial (hepatic) and caudal (cystic) parts.
- The hepatic primordium grows cranio-ventrally into the ventral mesogastrium and extends into the septum transversum.
- The endodermal hepatic diverticulum arises as a result of inductions originating from the hepato-cardiac mesoderm

LIVER

- The endodermal epithelial cells of the hepatic portion proliferate and form plates of liver cells.
- As development proceeds, the closely associated mesoderm of the septum transversum continues to support the sustained growth and proliferation of the hepatic endoderm.
- Hepatic growth factor, which is bound by the receptor c-met, located on the surface of the hepatic endodermal cells, is an example of a specific mesodermally-derived growth factor.
- Hepatic connective tissue arises from cells of the septum transversum and splanchnic mesoderm.

PANCREAS

- The pancreas develops as dorsal and ventral endodermal outgrowths of the caudal part of the foregut.
- The dorsal pancreatic bud, which develops before the ventral bud, occupies a position between the layers of the dorsal mesogastrium.
- The ventral pancreatic bud, which arises from the hepatic diverticulum near its origin, develops within the ventral mesogastrium.
- The cells of the pancreatic buds proliferate in an arboreal fashion and give rise to the ducts and associated secretory acini of the pancreas.

PANCREAS

- Some epithelial cells which lose their connections with the duct system develop into the endocrine portion of the pancreas, the pancreatic islets, known as islets of Langerhans.
- The connective tissue of the pancreas develops from splanchnic mesoderm.
- As a consequence of gastric and intestinal rotation, the ventral and dorsal pancreatic buds overlap and fuse at their points of contact.
- This fusion of the pancreatic buds results in a single anatomical structure consisting of a body and left and right lobes.

SPLEEN

- Although it is a lymphatic organ, development of the spleen is usually considered with the digestive system due to its close embryological association with the stomach, liver and pancreas.
- The mammalian spleen develops as an aggregation of mesenchymal cells in the dorsal mesogastrium.
- As the dorsal mesogastrium and stomach primordium rotate to the left, the spleen primordium is also drawn to the left and becomes apposed to the greater curvature of the stomach to which it is attached by a fold of the dorsal mesogastrium, the gastrosplenic ligament.
- The mesenchymal cells differentiate and form the splenic capsule and connective tissue; cellular elements of the spleen responsible for haematopoiesis derive from other haematopoietic centres, such as the aorta-gonad-mesonephros.

SPLEEN

- Later, with the establishment of definitive haematopoietic activity in the bone marrow and the development of the lymphoid component of the thymus, B and T lymphocytes populate the spleen and it becomes a functional lymphoid organ.

- By the third month of gestation, the principal structures of the bovine spleen, namely capsule, trabeculae, red pulp, white pulp and blood vessels, can be distinguished.

INTESTINE

- The intestines are formed from that portion of the foregut which is positioned caudal to the developing stomach and from the entire midgut and hindgut.

- A short section of the foregut has both a dorsal and ventral mesentery, while the ventral mesentery of the midgut and hindgut atrophies.

- The midgut, together with its associated mesentery, elongates forming a midgut loop.

INTESTINE

- At the ventral curvature of this loop, the vestige of the vitelline duct is evident.
- The descending limb of the midgut loop develops into the distal part of the duodenum, the jejunum and part of the ileum.
- The ascending limb forms the terminal portion of the ileum, the caecum, the ascending colon and the proximal portion of the transverse colon.
- The midgut receives its blood supply from a branch of the dorsal aorta, the cranial mesenteric artery, which is located in the dorsal mesentery.
- As the loop increases in length, it outgrows its available space in the abdominal cavity and occupies part of the extra-embryonic coelom called the umbilical sac.

INTESTINE

- This herniation of the foetal gut during this period of development, which is a normal occurrence, is referred to as physiological umbilical herniation.

- These changes occur around the third to fourth week of gestation in cattle, sheep, pigs and dogs.

- During the time the midgut loop occupies a position in the extra-embryonic coelom, it rotates clockwise, viewed dorso-ventrally, about an axis formed by the cranial mesenteric artery.

- The descending limb increases in length and forms a series of coiled loops on the right side of the umbilical sac.
- The ascending limb, which develops a diverticulum, the primitive caecum, grows more slowly than the descending limb and occupies the left side of the umbilical sac.
- Due to the lengthening of the midgut, the umbilical sac is unable to accommodate the herniated mass of intestines.

- Subsequently, the limbs of the midgut loop return to the abdominal cavity where they are accommodated, as the liver and kidneys occupy proportionally less space in the enlarged cavity than formerly.
- As the caecal diverticulum impedes the return of the ascending limb, the descending limb is first to return, passing to the left, caudal to the cranial mesenteric artery and occupying a position medial to the hindgut and its mesentery.
- As a result, the hindgut, destined to become the descending colon, moves to the left side of the abdominal cavity.

- The ascending limb of the midgut loop returns to the abdominal cavity passing in front of the cranial mesenteric artery and occupies a position to the right of the midline.

- The withdrawal of the midgut loop from the umbilical sac results in a further rotation of the intestine around the cranial mesenteric artery so that the full extent of rotation exceeds 270°.

HINDGUT

- The portion of the transverse colon which lies to the left of the median plane, together with the descending colon, the cloaca and the allantois, arise from the hindgut.
- The cloaca, the dilated terminal region of the embryonic hindgut, is partitioned by the formation of the urorectal septum into the anorectal canal dorsally and the urogenital sinus ventrally, and is separated from the proctodeum by the cloacal membrane.
- The allantois, which develops as an evagination of the hindgut, extends through the umbilicus and enlarges to occupy a position in the extra-embryonic coelom.

HINDGUT

- Fusion of the urorectal septum with the cloacal membrane divides the latter into two distinct membranes, the anal membrane dorsally and the urogenital membrane ventrally.

- An elevation covered by ectoderm surrounding the cloacal membrane, called the cloacal fold, also becomes subdivided into an anal fold dorsally and a urogenital fold ventrally.

- The urorectal septum gives rise to a fibromuscular mass referred to as the perineal body.

- Breakdown of both the anal and the urogenital membranes soon after their formation allows both the alimentary tract and the urogenital tract to communicate with the exterior.

- In domestic carnivores, two lateral epithelial outgrowths develop at the recto-anal junction and, from these, paranal sinuses and their associated circumanal glands are formed.