

Veterinary Bioscience: Digestive system

Lecture 26 – Development of the mouth and gastrointestinal tract in the embryo

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Key words

Embryology; gut tube; foregut; midgut; hindgut; mouth; palate; tongue; cloaca; gastrointestinal development; body cavities

Intended Learning Outcomes

At the end of this lecture you should be able to:

- Describe the derivatives of the primitive gut tube (fore-, mid-, hindgut) in order to explain the relations between organs in adult animals
- Explain the developmental anatomy in the embryo of the mouth and associated structures (including the tongue) in order to elaborate on the origin of anatomical structures in adult animals and explain common malformations
- Discuss the developmental anatomy of the oesophagus, stomach and intestines in order to elaborate on their orientation in adult animals.

The primitive gut and its derivatives

During **gastrulation**, three germ layers are formed: the **ectoderm**, the **mesoderm** and the **endoderm**. All tissues in the digestive tract (and most other systems) are derived from these three layers.

The **primitive gut tube** is derived from **endoderm** after the embryonic body starts folding into a cylindrical shape. It extends from the **oropharyngeal membrane** all the way to the **cloacal membrane** and contains three parts: the **foregut**, the **midgut** and the **hindgut**.

The parts of the primitive gut that remain outside the embryonic body wall form the **yolk sac** (midgut) and the **allantois** (hindgut).

Derivatives of the foregut include parts of the oral cavity, the pharynx, the oesophagus, the stomach, the proximal duodenum, the liver and pancreas, the thyroid, the parathyroid, the thymus, the trachea and lungs.

Derivatives of the midgut include the digestive tract from the duodenum to the transverse colon (supplied by the cranial mesenteric artery).

Derivatives of the hindgut include the distal part of the transverse colon to the descending colon (supplied by the caudal mesenteric artery) and the cloaca (→ anal canal / urogenital sinus)

Development of the mouth and associated structures

The **stomodaeum** is a midline depression of the ectoderm on the ventral surface of the head created by the cranial and lateral body folding. The **oropharyngeal membrane** separates the stomodaeum from the foregut and is thus composed of ectoderm and endoderm. This explains the ectodermal origin of the oral epithelium. When the oropharyngeal membrane breaks down, the cranial opening of the digestive tube is established.

After head folding, fleshy mesenchymal swellings, the **pharyngeal arches** (or branchial/ visceral arches), form on either side of the developing oro-nasal cavity. Their derivatives contribute to formation of the head and neck. The **first pharyngeal arch** divides into the left and right **maxillary processes** and **mandibular processes** which elongate to form the jaws and mouth.

Above the maxillary process another mesenchymal swelling, the **fronto-nasal prominence**, gives rise to the future frontal area of the embryo and the nose via the **frontal process** and the left and right **naso-lateral and naso-medial processes**. The frontal bones and the forehead are derived from the **frontal process**.

The upper jaw is formed by the naso-medial processes together with the maxillary processes.

The nose is formed by the frontal process together with the naso-lateral processes.

The lower jaw is formed by the fusion of the mandibular processes in midline.

At the point of fusion between the lateral nasal prominence and the maxillary prominence, the ectoderm canalizes and gives rise to the **nasolacrimal duct**.

Note the normal species variations in facial shape. As an example, **variations in the upper lip** are due to varying degrees of fusion between the medial nasal prominences:

- Sheep normally have a cleft upper lip
- Carnivores have a groove in the upper lip
- Horse/Cattle - have a smooth upper lip

Variations in the length of the face/skull are partly influenced by the groove between the medial nasal prominences and the length of fusions:

- **Dolichocephalic** - long faced (most species)
- **Brachycephalic** - short faced (certain dogs/ cats and primates)

Development of the palate

Initially, the **stomodaeum** forms as one indentation between the nasofrontal prominence and the first pharyngeal arch. The nasal pit deepens, and the mandibular prominence grows and merges. This results in the formation of two cavities, the primitive nasal and oral cavities. These are separated by the thin **oro-nasal membrane** (= **primary palate**) caudally and the **fused maxillary processes** cranially. When the **caudal portion of the oro-nasal membrane atrophies**, there is direct communication between the nasal and oral cavities. This is until **two lateral palatine processes** start forming. They are initially prevented from joining by the developing tongue, which protrudes into the nasal cavity. As the oral cavity expands and grows more than the tongue, the tongue no longer projects into the nasal cavity and the two palatine processes expand medially and merge in midline. This partition of the two cavities is referred to as the **secondary palate**. The rostral area of the palatine processes fuses with **the maxillary process**, sometimes also referred to as **medial palatine process**.

Development of the tongue

The tongue arises as a **protrusion from the floor of the pharynx** into the primitive mouth. Tongue formation begins as **4 distinct mesenchymal swellings**:

- one **median tongue swelling**
- two **lateral tongue swellings** and
- one **hypopharyngeal tongue swelling**.

The median and lateral tongue swellings will form the **body of the tongue** and are derived from **ectoderm**, while the hypopharyngeal tongue swelling will form the **root of the tongue** and is **endoderm**-derived. The **vallate papillae** demarcate the border between ecto- and endoderm derived parts.

The median tongue swelling is much larger in cattle than in carnivores and responsible for the **torus linguae** of the cow. The **sulcus** of the tongue in carnivores is located where the two lateral tongue swellings meet.

One indication that the tongue arises from several different origins are the many different cranial nerves innervating the different parts of the tongue.

Development of the oesophagus

The foregut narrows to form the oesophagus. Elongation of the oesophagus occurs during growth of the cervical and thoracic regions of the body. The **epithelial lining** of the oesophagus and any **associated mucosal glands** develop from the **endoderm** of the primitive foregut. The **connective tissue and muscle layer** of the oesophagus are derived from the **caudal pharyngeal arches (striated muscle)** and from the **splanchnic mesoderm** of the primitive gut (**smooth muscle**). The extent of the striated muscle contribution to the oesophageal musculature is species-specific.

Development of the stomach

The stomach arises as a **spindle-shaped swelling** of the foregut located in midline. A dorsal mesentery (the **dorsal mesogastrium**) develops on the dorsal surface and the ventral mesentery (the **ventral mesogastrium**) develops on the ventral surface. As the dorsal surface grows faster than the ventral parts, it develops into the **greater curvature**, while the **lesser curvature** develops on the ventral surface.

The developing stomach moves caudally and shifts away from the midline. Thus, the stomach **rotates** towards the left pulling with it the dorsal mesentery and leading to the formation of the **greater omentum**. The greater curvature moves **90 ° to the left** and then **45° in an anti-clockwise** direction about the dorso-ventral axis to rest ventrally.

There is species specific differential enlargement and reshaping of the stomach, e.g. the fundus of the equine stomach which extends markedly above the cardia as the saccus caecus.

Development of the bovine stomach

Initially, the bovine gastric primordium looks similar to that of monogastric animals: it has a dorsal greater and ventral lesser curvature and undergoes similar rotations. However, in ruminants the **fundic region** expands cranially and to the left forming the **primordia of the rumen and the reticulum**. An **evagination on the lesser curvature** forms the embryonic **omasum**. The **rumino-reticular groove** forms on the ventral surface and the **cranial** and **caudal grooves** start to partially separate the ruminal sacs. The embryonic rumen rotates 150° from a cranio-dorsal position to a caudal position to the left of midline. As it folds over during this rotation, it moves the other gastric compartments and the intestines towards the right.

Development of the pancreas

The pancreas is derived from two primordia:

- the **dorsal primordium** from the **dorsal duodenum** forms the **left lobe**
- the **ventral primordium** from the **hepatic diverticulum** forms the **right lobe**

Due to the gastric and intestinal rotation, the two primordia move together and fuse. This explains the **species-specific duct systems**: In horses, dogs and humans, both pancreatic ducts persist in their entirety. The pancreatic duct from the ventral lobe joins the bile duct before opening onto the major duodenal papilla. The accessory pancreatic duct from the dorsal lobe opens onto the minor duodenal papilla. In sheep, goats and cats, the terminal portion of the dorsal duct atrophies, while in cattle and pigs the terminal portion of the ventral duct atrophies instead.

Development of the small and large intestines

Initially the primitive gut is straight with dorsal and ventral mesenteries. Later, the ventral mesentery atrophies. For a while, the gut grows faster than the body, so a **hairpin-shaped loop** is forced out of the abdominal cavity (which is primarily occupied by the large liver at this stage) into the umbilical stalk. This is referred to as **physiological umbilical herniation**. A connection to the remnant of the yolk sac (the yolk-stalk) is at the tip of the loop.

During the time of the herniation, the midgut loop **rotates** approximately **180 degrees** clockwise. When the loop gets pulled back into the abdominal cavity, it rotates further so that the final rotation exceeds **270 degrees**.

Further changes involve **extensive coiling** of the cranial arm of the loop to form the duodenum, jejunum and most of the ileum.

The gut loop from the yolk-stalk to the proctodaeum contributes to the terminal part of the ileum, caecum, colon, rectum and anal canal. The caecum becomes established as a definite pouch-like diverticulum of the digestive tube. Changes occur in the developing caecum and colon to evolve into the species-specific final shapes and locations, such as the double horseshoe-shaped colon in the horse.

Development of the cloaca and proctodaeum

The caudal portion of the primitive gut expands to form the blind cavity of the **cloaca**. The invagination of ectoderm beneath the tail forms the **proctodaeum**. The **cloacal membrane** consists of ectoderm and endoderm similar to the oropharyngeal membrane in the front of the embryo. When the cloacal membrane degenerates, the **anal opening** is formed. The terminal end of the developing gut enters the dorsal cloaca and forms the **primitive anorectal canal**. The **allantois** is a ventral outgrowth of the caudal primitive gut and forms the **primitive urogenital sinus** which later forms the bladder, urachus and parts of the reproductive tract. The **urorectal septum** is formed to separate the anal from the urogenital sinus.

Further reading

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