INSECT MORPHOLOGY - DIGESTIVE SYSTEM

* The digestive system is also commonly referred to as the alimentary canal. The alimentary canal is a tube, usually coiled, which extends from the mouth to the anus, and consists of three regions: the **foregut, midgut, and hindgut.** The foregut is also known as the **stomodaeum**; the midgut is also known as the **mesenteron**; and the hindgut is also known as the **proctodaeum.** Each of these regions may be divided into two or more subregions; and there are usually valves and sphincters between these regions which regulate the passage of food from one region to another. As we mentioned in our last lecture the stomodaeum and the proctodaeum are ectodermal in origin and the mesenteron is endodermal in origin.

PREORAL CAVITY

* The mouthparts lie close together and form a small cavity often called the mouth cavity. Since it lies anterior to the true opening to the stomodaeum it is more properly known as the preoral cavity [Snodgrass]. The true mouth is the opening of the stomodaeum. This preoral food chamber is also sometimes called the **cibarium**. There are usually muscles attached to the **cibarium** that have their other origins inserted on the clypeus (they are located anterior or ventral to the frontal ganglion) - these are called the **dilators of the cibarium**.

FOREGUT

* Since the foregut is ectodermal in origin it is lined with a layer of cuticle, known as the **intima**, which is shed at each molt in the same way as the rest of the cuticle. The foregut epithelium consists of flattened cells with indistinct boundaries. Outside the epithelium is a layer of longitudinal muscle and a layer of circular muscle, the latter often being relatively well developed. The circular muscles are not inserted into the epithelium, but are continuous around the gut so that when they contract the epithelium becomes longitudinally folded. When the gut is distended with food these folds are flattened out. In addition, especially in the proventriculus, there may be 6-8 permanent infoldings of the wall. The longitudinal muscles may be inserted into the circular muscles or into the epithelium. Outside the muscle layers is a delicate connective tissue sheath.

Buccal Cavity:

* This is the initial region just within the mouth and is often indistinguishable from the pharynx. It is the oral part of the stomodaeum and should not be confused with the cibarium.

Pharynx:

* The first part of the foregut is the **pharynx** which connects anteriorly with the buccal cavity. In general the pharynx is that part of the foregut that lies within the head and for the most part beneath and in front of the brain. The pharynx has associated with it a set of muscles called **precerebral dorsal dilator muscles of the pharynx** (or sometimes just called the **dilators of the pharynx**) which arise ventrally on the tentorium and dorsally from the frons. They insert on the pharynx posterior to (or above) the **frontal ganglion**. These are best developed in sucking insects, especially in Lepidoptera and Hymenoptera which use the pharyngeal pump to draw up fluids. They are also present in biting and chewing insects and play a part in passing food back from the mouth to the oesophagous. The **frontal ganglion** of the **stomodaeal nervous system** lies on the pharynx just above the mouth. In some insects the pharynx is divided into 2 regions called the **anterior pharynx** and the **posterior pharynx**.

Oesophagus:

* The next part of the foregut is the **oesophagus** which is an undifferentiated part of the foregut serving to pass food back from the pharynx to the crop. In the simplest case it is a simple tube leading from the pharynx to the midgut, but usually it is regionally differentiated, in which case only the tubular region lying just posterior to the pharynx is called the oesophagus.

Crop:

* The **crop** or **ingluvies** is an enlargement of the foregut in which food is stored. Usually it represents the posterior part of the oesophagus, but in some fluid feeders (Diptera and Lepidoptera) it is a lateral diverticulum.

Often the crop is folded longitudinally and transversely when it is empty. In general, secretion and absorption do not occur in the crop, being limited by the impermeable intima. Digestion can occur, however, as a result of salivary enzymes passing back to the crop with the food and midgut enzymes being regurgitated from the midgut. Although the proventriculus acts as a valve limiting the backward movement of food, it does not prevent the regurgitation of fluids.

Proventriculus:

* The next structure is the **proventriculus**. This structure can be quite variable. In fluid feeders it is often absent except for a simple valve at the origin of the midgut. A valve is also present in many other insects and often the circular muscles form a sphincter at the entrance to the midgut. This valve or sphincter is called the **esophageal** or **cardiac valve**. The proventriculus often has on its internal surface sclerotized structures for the grinding of food. For example, in the cockroach and cricket the intima is developed into six strong plates or teeth, which serve to break up the food. The proventiculus as a whole controls the passage of food from the crop to the midgut.

* The proventriculus is very specialized in bees. An anterior invagination into the crop ends in four mobile lips each armed with a number of spines. Again the proventriculus controls the movement of food from the crop to the midgut, but it is also able to remove pollen from a suspension in nectar in the crop while the nectar is retained. Writhing movements of the crop keep the pollen dispersed while the lips of the proventriculus make snapping movements in such a way that the spines strain off the grains of pollen and retain them. In this way a bolus of pollen is formed and is then passed back through the proventriculus to the midgut. Nectar is retained in the crop for regurgitation and processing to form honey.

MIDGUT

General - The middle section of the alimentary canal is the stomach and is commonly called the **ventriculus**. This is the portion of the alimentary canal where digestive juices are secreted, and as such this is where most of the digestion takes place. This portion of the alimentary canal begins at the posterior foldings of the stomodaeal valve, the line being marked by the termination of the stomodaeal intima. Posteriorly the midgut ends just anterior to the Malpighian tubules. The midgut is usually a simple tube, undifferentiated except for the presence of 4, 6, or 8 caeca at the anterior end called **gastric caecae**. Gastric caecae may occur on other parts of the midgut also. In some Diptera, the midgut is differentiated into an anterior cardiac chamber (Snodgrass called it this, but other authors call it the proventriculus) and a long ventriculus. In the Heteroptera there are 4 regions, the last giving rise to numerous caecae which house bacteria.

* The most characteristic cells of the midgut epithelium are tall and columnar with microvilli forming a striated border bounding the lumen. Typically, the basal membrane is very deeply infolded and large numbers of mitochondria are associated with the folds. Rough endoplasmic reticulum is also often extensive and it is probable that this is concerned with enzyme production. There may be several different cell types present. For example, there may be **lipophilic cells** which are packed with lipoid spheres and glycogen, and the striated border consists of parallel lamellae rather than microvilli. In these cells the mitochondria are rather uniformly distributed. Another type of cell is a **cuprophilic cell** which contain esterases and cytochrome oxidase and the microvilli are sparse and squat. Mitochondria are associated with the infoldings of the basal membrane.

* The columnar cells are concerned with enzyme secretion and with absorption. During secretion granules appear in the cytoplasm and these give rise to vacuoles which may be liberated separately into the gut lumen through the striated border or they may first coalesce into a single large vacuole. Secretion may involve the complete breakdown of the cell which is then replaced by the regenerative cells. Such breakdown may occur randomly throughout the gut or it may pass in waves along the length of the epithelium. Secretion that involves the complete breakdown of a cell is called **holocrine secretion.** When the cell does not breakdown completely, but recovers and functions again, the process is known as **merocrine secretion.**

* In some insects (Lepidoptera caterpillars, Ephemeroptera, and Plecoptera) there are also **goblet cells** in addition to the columnar cells. Goblet cells probably play a role in secretion, but they appear to also be involved in storage secretion. In some Lepidoptera they accumulate metals and dyes in the goblet cavity or in the cytoplasm of the cell. These substances are discharged at the following molt when the whole of the epithelium is renewed.

* As mentioned earlier there are also regenerative cells present to replenish the columnar cells when they breakdown during secretion. These regenerative cells are small cells lying at the base of the epithelium either scattered or in groups called **nidi**. Sometimes they occur at the bottom of folds or **crypts** in the epithelium.

* The muscle layers of the midgut are usually poorly developed, but the circular muscles lie adjacent to the epithelium, which is the reverse of the position in the foregut. The muscle layers are bounded by a delicate connective tissue sheath.

Peritrophic membrane:

* The midgut does not have a cuticular lining, but in most insects, it is lined by a delicate **peritrophic membrane**. It is absent in many fluid-feeding insects and in a few Coleoptera. There are 2 types of peritrophic membrane classified by the way it is produced. In some Diptera it is secreted as a viscous fluid at the anterior end of the midgut. This fluid is forced through a mold or press formed by the stomodaeal invagination and the wall of the midgut so that it forms a tube which becomes the membrane. This type of membrane is formed continuously, and is usually composed of a single layer of disoriented fibers in an amorphous matrix. The second type of membrane is formed by delamination from the whole surface of the midgut. This type occurs in Orthoptera, Odonata, Coleoptera, and Hymenoptera, and there is often several membranes lying one inside the other. The function of the peritrophic membrane is to protect the cells from damage by the gut contents and this is consistent with its absence or delicate nature in many blood-feeding insects. In general the membrane acts as a barrier to microflora so that infection is prevented, and it may also facilitate absorption in fluid feeders. It will allow the passage through it of water, salts, glucose, and amino acids, but it will allow the passage of enzymes only inward from the outside, but not back to the outside from the inside.

Filter chamber:

* The Homoptera and some Heteroptera feed on fluids and as such they must ingest large quantities of fluid. The gut has undergone modifications to handle the large intake of fluids and the need for rapid elimination of large quantities of excess water. This is necessary to avoid excessive dilution of the haemolymph and to concentrate the food to facilitate enzyme activity. In the Cicadoidea the rapid removal of water to the large rectum is achieved by the anterior midgut forming a large thin-walled bladder which is closely bound to the anterior hindgut and Malpighian tubules by its own basement membrane. The chamber formed within the folds of the anterior midgut is called the **filter chamber**. Water passes directly from the midgut to the hindgut along an osmotic gradient.

HINDGUT

* The hindgut is lined by a layer of cuticle which is thinner and more permeable than that of the foregut. The epithelium generally is thin, but the cells are more cuboid than in the foregut while those of the rectal pads are tall with a clear cytoplasm. The musculature is poorly developed except around the rectum, but where it is present the longitudinal muscles are usually external to the circular. Along the rectum the longitudinal muscles are often collected into strands opposite the gaps between adjacent rectal pads.

Pylorus:

* The pylorus is the first part of the hindgut and from it the Malpighian tubules often arise. In some insects it forms a valve between the midgut and hindgut. This valve is called the **pyloric valve** or the **proctodaeal invagination**. It is on the pylorus that the **Malpighian tubules** open. These serve an excretory function and will be discussed in more detail later.

Ileum:

* The hindgut in general is divided into two main regions; the first is the **anterior intestine**. Sometimes the anterior intestine may be divided into an anterior **ileum** and a posterior **colon**. In most insects the ileum is an undifferentiated tube running back to the rectum, but in some termites it forms a pouch in which the flagellates concerned with cellulose digestion live, and in some larval Scarabaeoidea there is a comparable fermentation chamber in which the intima is produced into spines. It is believed the ileum is involved in the removal of water from the haemolymph in Heteroptera, and is some Diptera it is thought to aide in the excretion of ammonia.

Rectum:

* The second main region of the hindgut is the **posterior intestine** or **rectum**. The rectum is the terminal structure and opens externally through the **anus**. The rectum is often an enlarged sac and is thin walled except for certain regions, the **rectal pads**, which have a columnar epithelium. There are usually 6 rectal pads and they may extend longitudinally along the rectum or they may be papilliform. Each pad may consist of a single layer of cells (Odonata, Orthoptera) or there may be 2 layers (Neuroptera, Lepidoptera, Hymenoptera). The pads have a good tracheal supply indicating a high level of metabolism.

* The rectum, and in particular the rectal pads, are important in the reabsorption of water, salts and amino acids from the urine. In addition in some aquatic insects, there are tracheal gills in the rectum. In larval Anisoptera water is pumped in and out of the rectum so that the water round the gills is constantly renewed, and by the forcible ejection of water the insect is able to propel itself forwards rapidly.

Movement of food through the gut:

* Food is pushed back from the pharynx by the pharyngeal pump, aided by the cibarial pump when this is present, and subsequently passed along the gut by peristaltic movements. The movement of food from the crop to the midgut is controlled by the proventriculus and the associated sphincter. In the midgut the passage of the food is aided by the peritrophic membrane which, as it moves down the gut, will carry the enclosed food with it.

Head glands:

* Associated with the mouthparts are the mandibular, maxillary, pharyngeal, and labial glands although they are not usually all present together.

* **Mandibular glands** - Found in Aptergota, Isoptera, Coleoptera, and Hymenoptera. They are usually sac-like structures in the head near the bases of the mandibles. In *Apis*, the glands are larger in the queen than in the worker and are very small in the drone. In the queen, they produce the pheromones concerned with colony control, while in workers they probably produce some saliva and serve to soften the coccoon (breakdown silk) at the time of emergence. They are also quite large in larval Lepidoptera where they are the functional salivary canals, but they are absent from adult Lepidoptera.

* **Maxillary glands** - Found in Protura, Collembola, Heteroptera, and some Neuroptera and Hymenoptera. They are usually small, opening near the bases of the maxillae, and they may be concerned with the lubrication of the mouthparts. In carnivorous Heteroptera, they may play a part in producing the toxin which kills the prey.

* **Pharyngeal glands** - [Snodgrass calls the hypopharyngeal glands]. Found in Hymenoptera and particularly well developed in worker honeybees. They are vestigial in the queen and absent in the male. There is one gland on each side of the head, each consisting of a long coiled tube to which large numbers of solid lobules are attached. The glands open at the base of the hypopharynx by separate ducts. They produce brood food with which young larvae are fed and which probably plays some part in caste determination.

* **Labial glands** - These are found in most insects; absent from some Coleoptera. They are large and extend back into the thorax. In most insects the labial glands are **acinuous glands** (a cluster of connected spheres, like a

cluster of grapes), the acini containing 2 cell types. In larval Diptera the cells are enormous and contain polytene chromosomes. Part of the gland may be differentiated to form a salivary reservoir, while in the Heteroptera the gland consists of a number of separate lobes. Anteriorly the glands open into a narrow duct on each side and these join to a single median opening into the **salivarium**. In fluid-feeding insects the salivarium is modified to form a pump. This has a rigid lower wall and a flexible upper one which can be drawn upwards by dilator muscles so that fluid is sucked into the lumen and then, when the muscles relax, the upper wall springs down by virtue of its elasticity and forces saliva out.

* In most insects the labial glands are the functional salivary glands. The saliva serves to lubricate the mouthparts, more is produced if the food is dry, and it also contains enzymes which start the digestion of food. The saliva of some blood-sucking insects also contain an anticoagulant. In larval Lepidoptera and Trichoptera the labial glands produce silk which is used in the construction of larval shelters and the coccoon. Silk consists of an inner tough protein called **fibroin** which is enclosed by a water-soluble gelatinous protein called **sericin.**