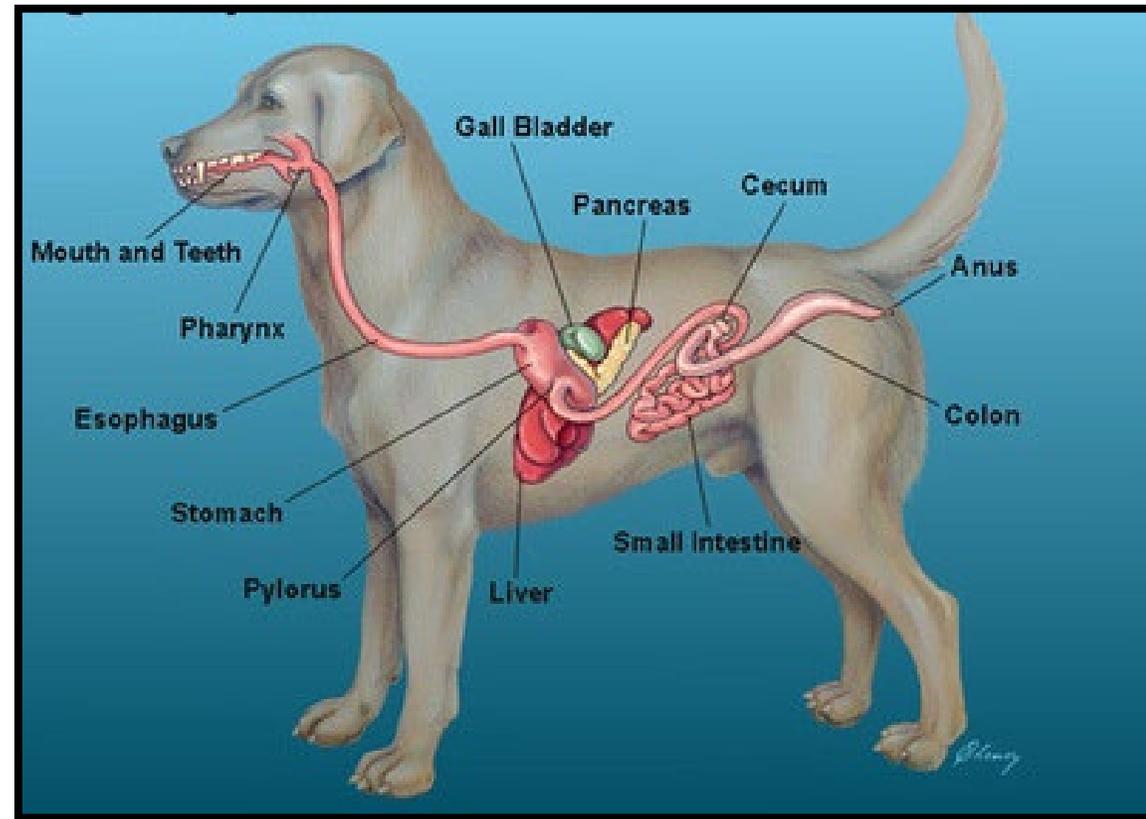


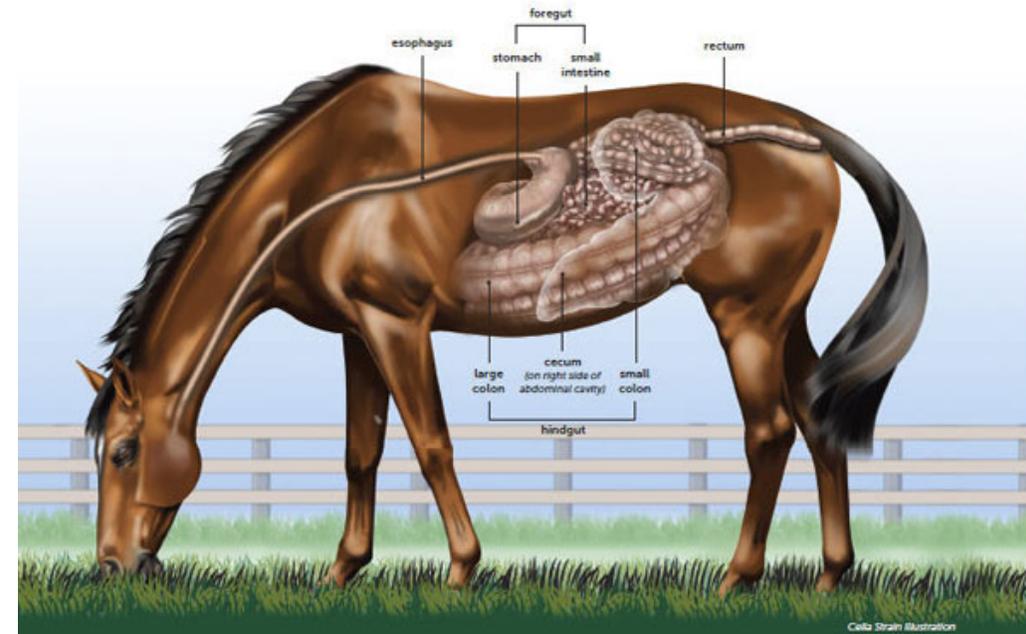
DIGESTION&ABSORPTION



ASSOC. PROF. YASEMIN SALGIRLI DEMIRBAS

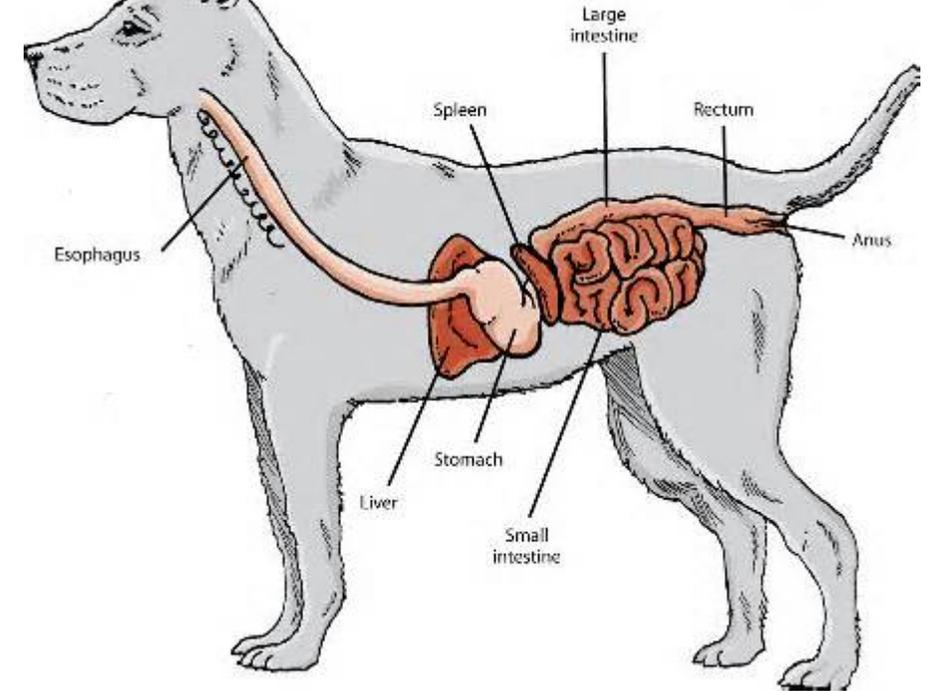
Digestion

- Digestion is the breakdown of food into smaller components that can be more easily absorbed and assimilated by the body
- These smaller substances are absorbed through the small intestine into the blood stream
- Digestion is a form of catabolism that is often divided into two processes based on how food is broken down:
 - 1. Mechanical digestion
 - 2. Chemical digestion
- Mechanical digestion refers to the physical breakdown of large pieces of food into smaller pieces which can subsequently be accessed by digestive enzymes.
- In chemical digestion, enzymes break down food into the small molecules the body can use
- The functions of the gastrointestinal system can be described in terms of these four processes—digestion, secretion, absorption, and motility



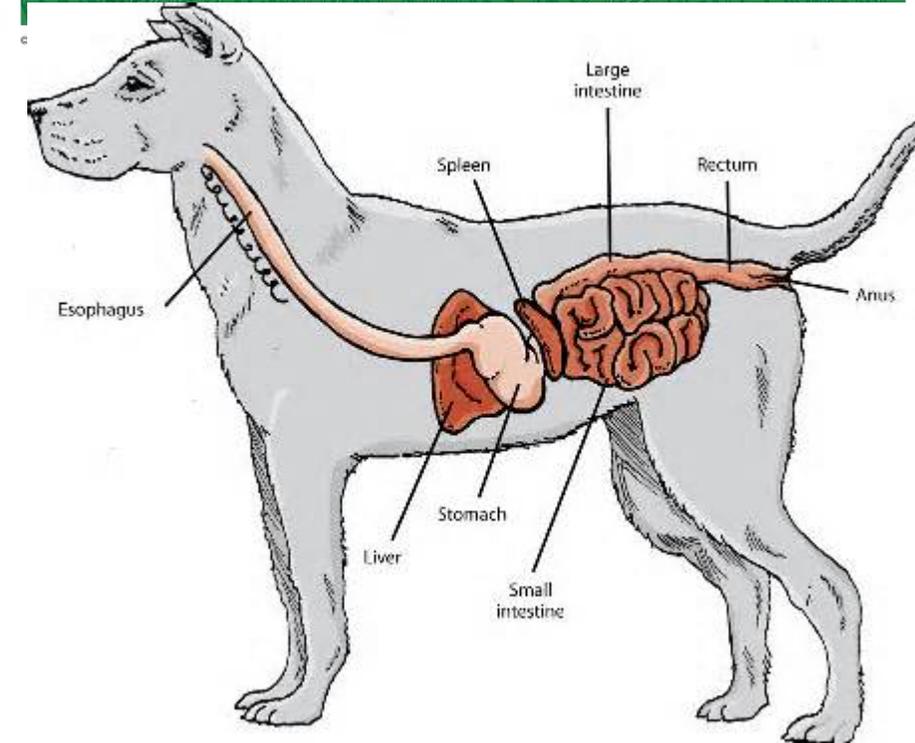
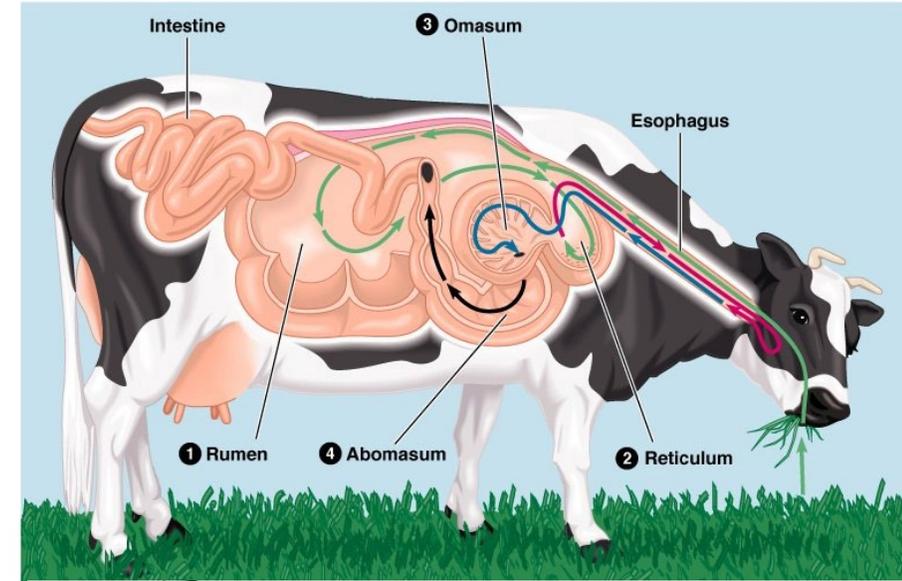
Gastrointestinal Motility

- The digestive tracts of all animals have evolved to perform several major functions.
- The main function is to digest and absorb the nutrients of the diet needed to sustain the rest of the body.
- It is important to recognize that the lumen of the digestive tract is actually contiguous with the exterior environment.
- Lumen of the gut serves as an ecological niche for a wide variety of bacteria and, in some species, fungi and protozoa to thrive in.
- A major function of the gut is to identify and prevent entry of pathogens across the gut epithelium barrier.
- Another function of the digestive tract is the elimination of wastes:
 - ✓ includes undigested material from the diet and removal of toxicants from the blood.
- Three basic types of digestive tract systems are described in detail: **simple-stomached animals (including dogs and cats)**, **forestomach fermenters (ruminants and camelids)**, and **hindgut fermenters (such as the horse and rabbit)**.



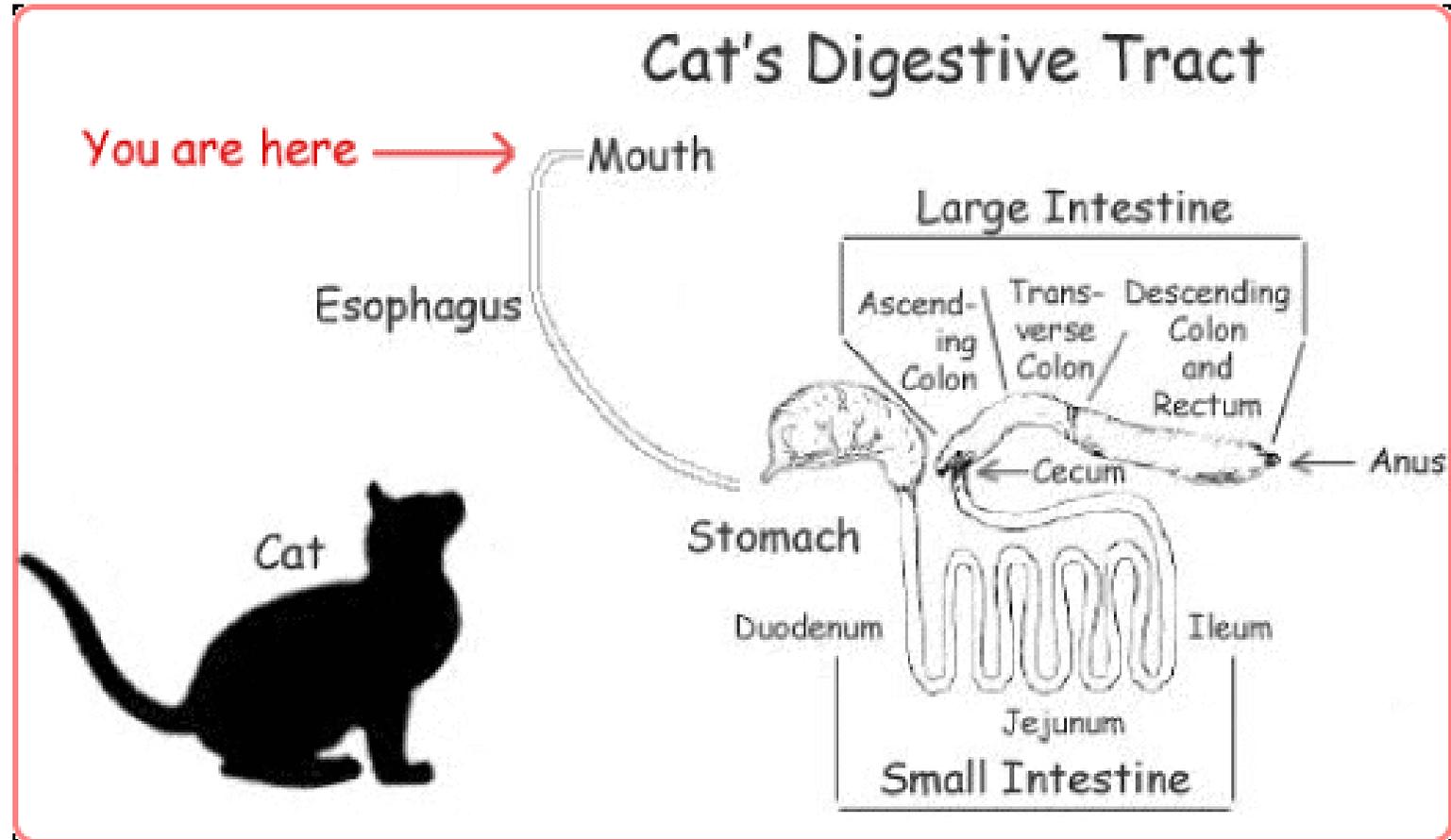
Gastrointestinal Motility

- Monogastric animal different from Ruminant animal:
 - ✓ I. A monogastric organism has a simple single-chambered stomach
 - ✓ II. Ruminant organism, like a cow, goat, or sheep, which has a four-chambered complex stomach
 - ✓ III. Monogastrics cannot digest the fiber molecule cellulose as efficiently as ruminants
 - ✓ IV. No rumination like ruminant animal
 - ✓ V. A monogastric digestive system works as soon as the food enters the mouth
 - ✓ VI. Saliva moistens the food and begins the digestive process.
 - ✓ VII. After being swallowed, the food passes from the esophagus into the stomach, where stomach acid and enzymes help to break down the food
 - ✓ VIII. While in ruminant, it undergoes degradation by means of microbes like protozoa, bacteria, fungus
 - ✓ IX. Bile salts stored in the gall bladder empty the contents of the stomach into the small intestines where most fats are broken down.



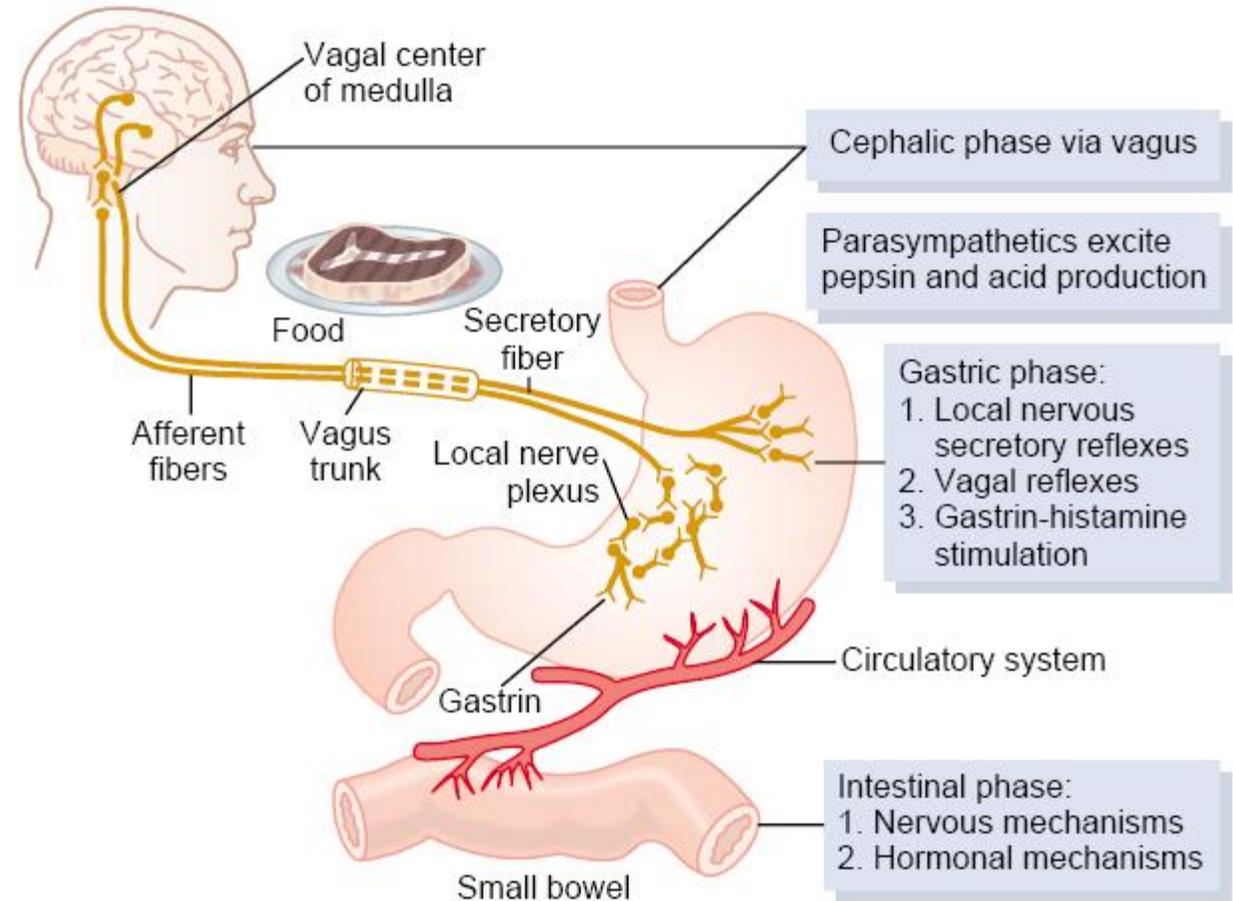
Digestive tract

- **Consist of 6-main parts:**
- 1. Mouth
- 2. Esophagus
- 3. Stomach
- 4. Small Intestine (SI)
- 5. Large Intestine (LI)
- 6. Supportive organs:
 - a. Liver
 - b. Pancreas
 - c. gall bladder



Phases of Gastrointestinal Control

- The neural and hormonal control of the gastrointestinal system is, in large part, divisible into three phases—cephalic, gastric, and intestinal—according to stimulus location.
- **The cephalic phase** is initiated when receptors in the head (cephalic, head) are stimulated by sight, smell, taste, and chewing. It is also initiated by various emotional states.
- Four types of stimuli in the stomach initiate the reflexes that constitute the **gastric phase of regulation**: distension, acidity, amino acids, and peptides formed during the digestion of ingested protein.
- The responses to these stimuli are mediated by short and long neural reflexes and by release of the hormone gastrin.
- Finally, **the intestinal phase** is initiated by stimuli in the intestinal tract: distension, acidity, osmolarity, and various digestive products.
- The intestinal phase is mediated by both short and long neural reflexes and by the gastrointestinal hormones secretin, CCK, and GIP, all of which are secreted by endocrine cells in the small intestine.



The oral cavity

- The structures of the oral cavity are necessary for:
 - ✓ prehension of food,
 - ✓ mastication of the food material, and
 - ✓ swallowing of the material while protecting the animal from inhalation of the foodstuffs.
- Many strategies for moving food into the oral cavity have evolved:
 - ✓ In horses upper and lower lips are quite flexible and sensitive
 - ✓ Pigs use their lower lips in a similar fashion.
 - ✓ Ruminant lips are not very flexible and have limited ability to grasp food. Instead they have tongues to grasp herbivorous material.
 - ✓ Dogs, cats, and many other carnivores grasp food with their teeth and move their open mouth forward to catch the food in the more caudal aspect of their oral cavity until it can be swallowed. .



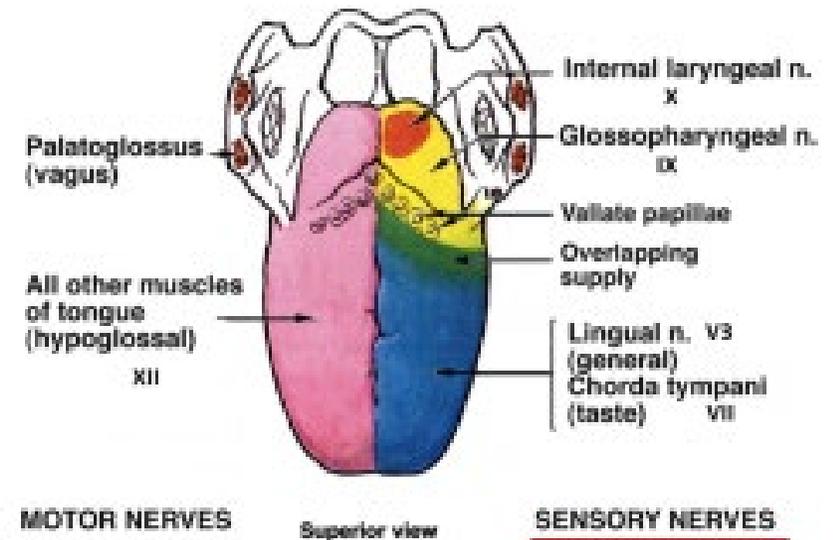
The oral cavity

- Species also differ in how they drink water.
- Horses and cattle, like humans, can create a negative pressure within the oral cavity that allows suction of water to the back of the oral cavity.
- Cats, dogs, and their wild relatives cannot develop negative pressure within their oral cavity due to elongated snouts and inability to tightly close the lips at the commissure of the mouth.
- These species must lap water.
- This is done rapidly and repeatedly, since a dog for example may draw up just 10–15 mL of water with each lap.



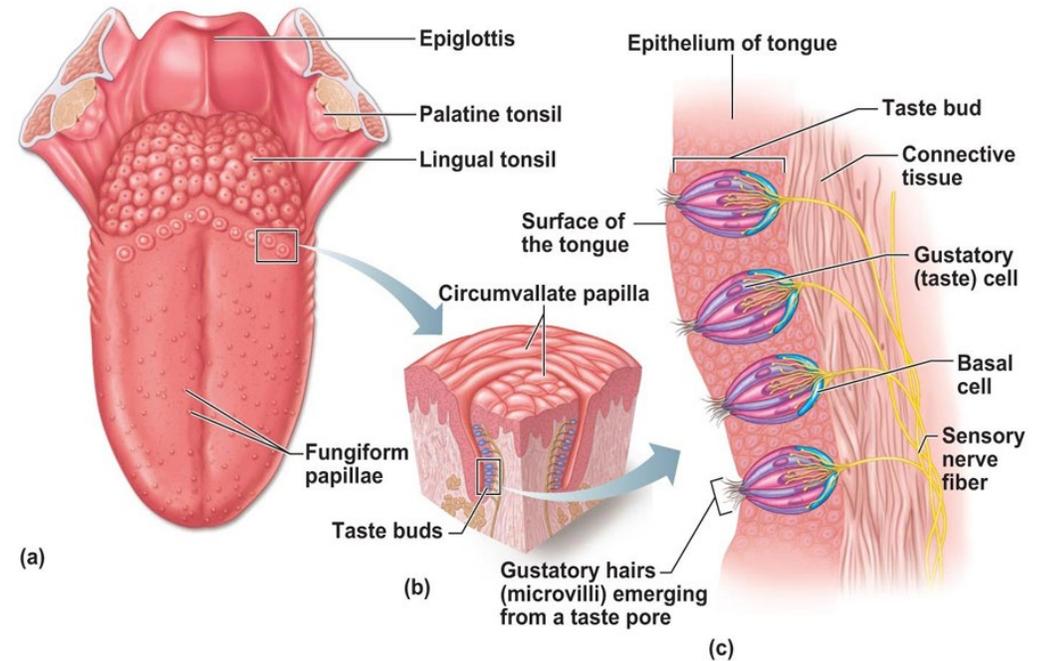
The tongue

- The tongue has bundles of muscles that run in nearly all directions that allow great flexibility and direction of movement.
- There are also muscles attached to the posterior tongue that help retract and depress or elevate the tongue.
- The motor functions of the tongue are nearly all controlled by motor neurons of the hypoglossal or cranial nerve XII.
- In addition to movement, the tongue has a major sensory role.
- The rostral two-thirds of the tongue is innervated by the sensory lingual branch of the trigeminal (cranial nerve V), which is sensitive to temperature, touch, and pain, and the facial nerve (cranial nerve VII), which transmits a sensation of taste and carries parasympathetic fibers to the base of the taste buds.
- The caudal one-third of the tongue is innervated by the lingual branch of the glossopharyngeal nerve (cranial nerve IX) which carries taste sensation from taste buds, and parasympathetic efferent fibers to the taste buds.



The tongue

- Tongues have various types of papillae, depending on species.
- These are mainly used to help propel food to the back of the oral cavity, though they are also useful for grooming (cat).
- A unique feature of the tongue is the taste bud.
- Food particles proceed into the cleft between tongue papillae and can enter each taste bud through an opening pore.



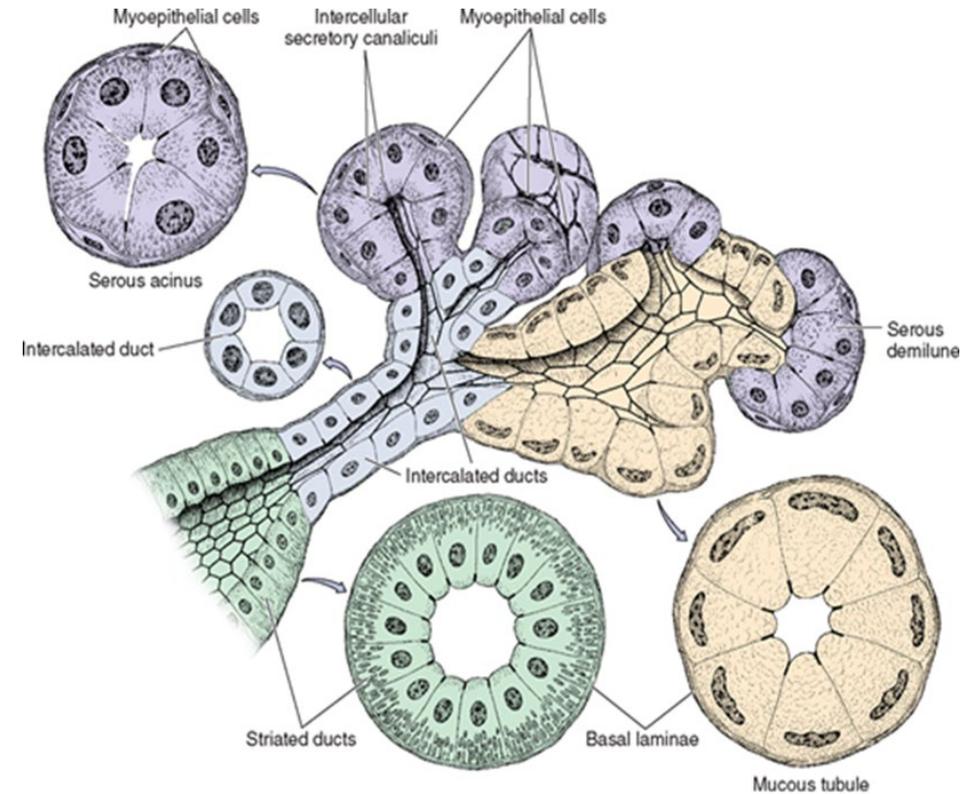
Mastication

- Mastication of the diet can greatly aid the digestibility of the ingested material.
- The incisors of the dental arcade are important for cutting foodstuffs into a size that can be brought into the oral cavity.
- The premolars and molars are capable of reducing the ingested material into much smaller and finer particles that increase the surface area available for digestive enzymes to act upon.
- This is particularly important for digestion of herbivorous materials.
- Plant cell walls need to be broken open and chewing with molars can initiate this process in the larger herbivores.



Salivary secretions

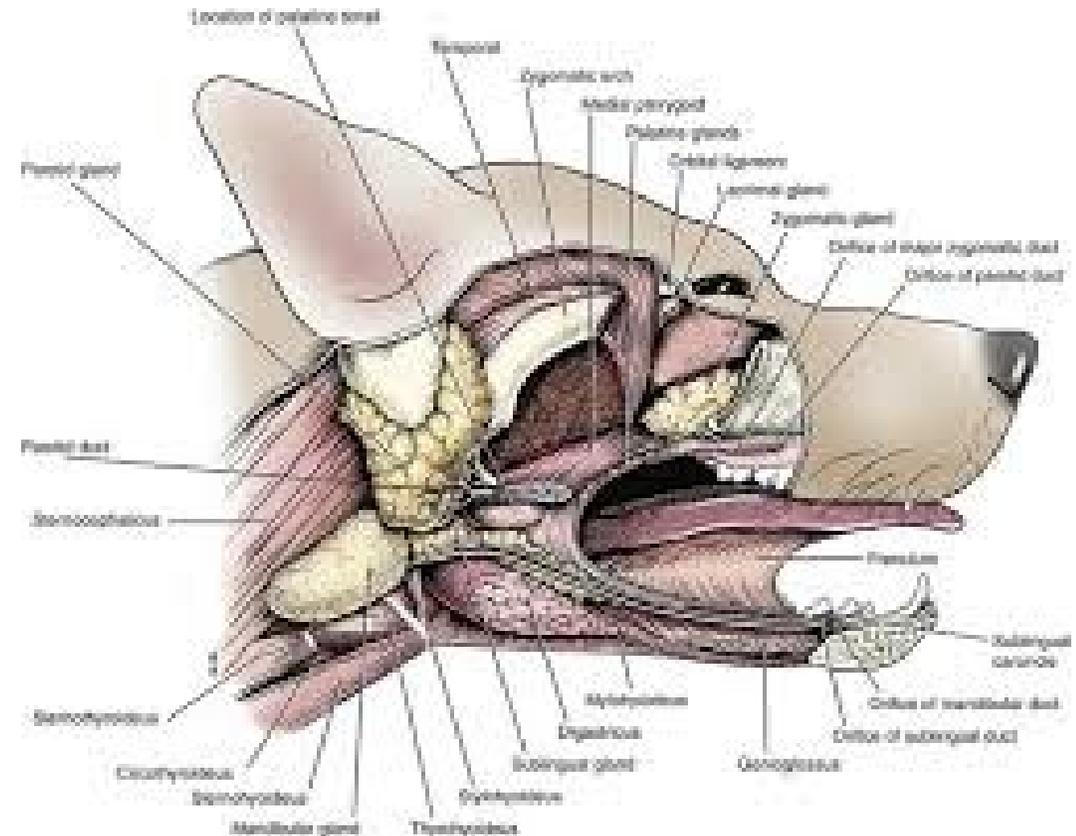
- As a bolus of food is being chewed, saliva is added.
- Saliva is produced by acinar glands located along the mandible and maxilla of most species.
- The secretions of the acinar cells are conducted by a series of ducts, beginning with intercalated ducts that lead to slightly larger striated ducts which then join with intralobular and interlobular ducts until finally the secretions reach the oral pharynx.
- The secretions of individual salivary glands range from a watery composition referred to as a serous secretion to a more mucoid secretion.



Source: Mescher AL: Junqueira's Basic Histology, 13th Edition: www.accessmedicine.com
Copyright © The McGraw-Hill Companies, Inc. All rights reserved.

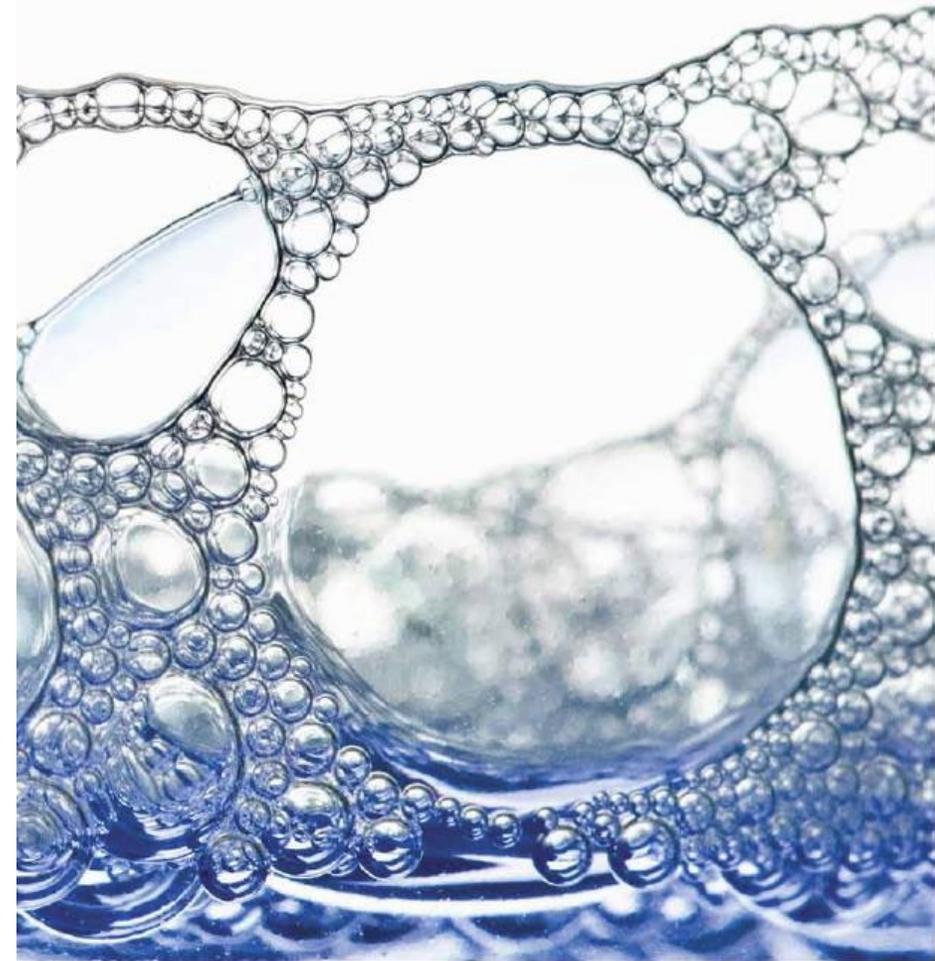
Salivary secretions

- For instance in the dog the **parotid gland** produces a **serous secretion** laden with amylase, which begins the process of starch digestion, and buffers to help control the pH of the ingesta. A lipase enzyme is also present to initiate fat digestion.
- Serous glands also secrete **IgA** and antibacterial substances such as **lysozyme** that also help keep bacterial numbers in check within the oral cavity.
- The **sublingual glands** of a dog produce a **mucus-type saliva**.
- The mucin helps lubricate the bolus as it passes down the esophagus.
- The **submaxillary gland** of the dog produces a mixed secretion that has both serous and mucous attributes.
- A 20-kg dog produces approximately 0.5–1 L of saliva daily, more when fed a dry dog food.
- All saliva is hypotonic to help reduce the osmotic concentration of the ingesta.



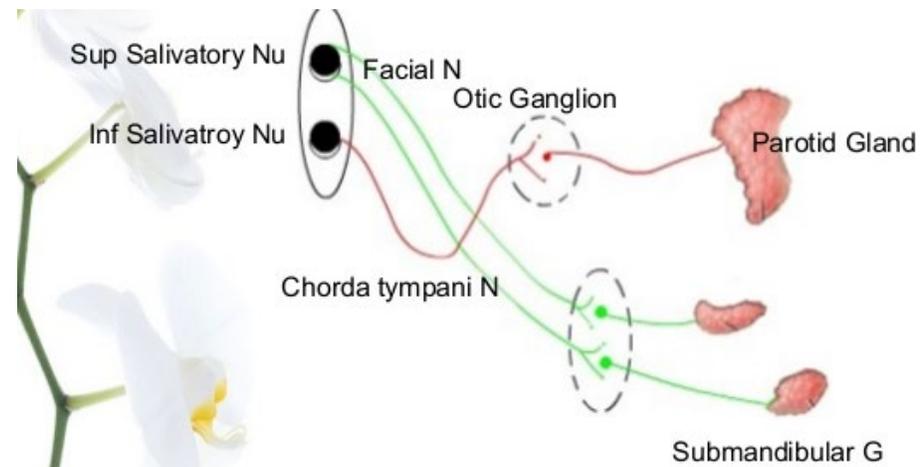
Salivary secretions

- Composition and Function of saliva(mouth)
- 99% water
- Mucus → lubrication aid for swallowing
- Bicarbonate salts (Na) → buffer to regulate pH of stomach
- Amylase enzyme in some species (Human-strong activity Pigs- limited Horses- not exist)
- Function of Saliva:
 1. Lubricant
 2. Protection of membranes in mouth
 3. Digestion (amylase)
 4. Thermoregulations (dogs-panting; cats-grooming).



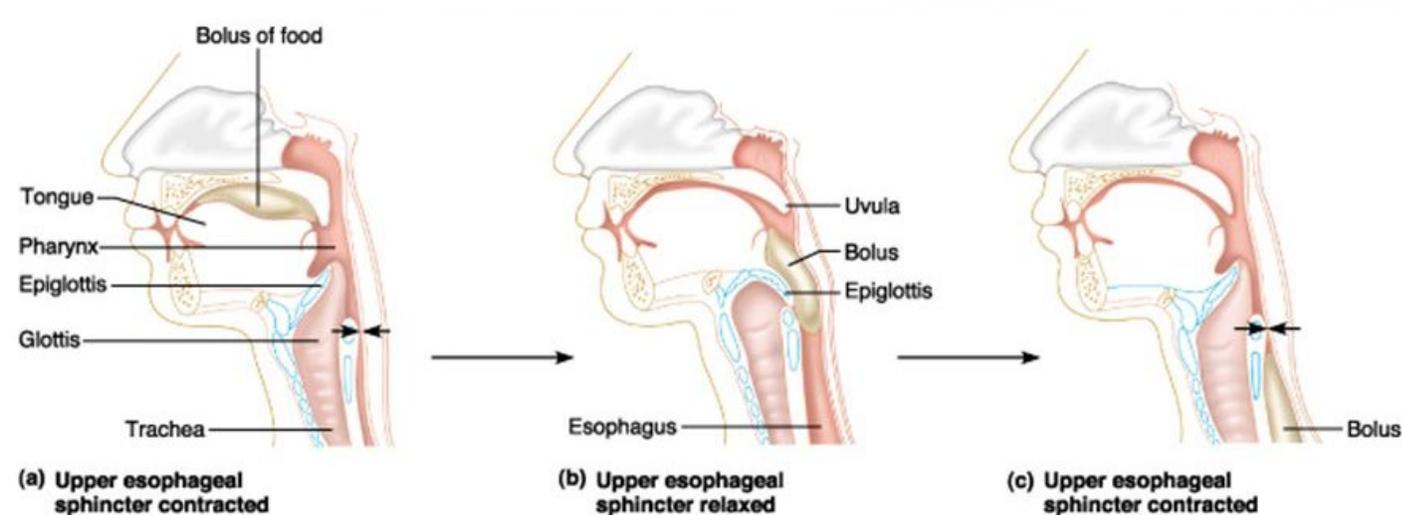
Salivary secretions

- Salivary secretions are under the control of the glossopharyngeal nerve (parotid glands) and the facial nerve (submaxillary and sublingual glands).
- These nerves carry parasympathetic fibers and it is the parasympathetic tone that determines the rate of saliva production and secretion.
- Secretion occurs when myoepithelial cells respond to parasympathetic stimulation and squeeze the acinus to propel saliva down the ducts.
- There is no sympathetic innervation of the salivary glands.
- As Pavlov demonstrated, higher centers of the brain can activate parasympathetic pathways to cause a dog to drool in anticipation of a meal.



Deglutition (swallowing)

- Once the bolus of food has been chewed and is moistened by saliva and moved to the back of the oral cavity it is ready to be swallowed.
- Deglutition is a highly complex reflex that must deliver ingesta or fluids to the esophagus while keeping such material out of the respiratory tract.
- The pathway of airflow into the trachea and the pathway for food entering the esophagus intersect within the pharynx.
- The first step in swallowing is voluntary: the animal uses motor neurons to push the bolus of food to the back of the tongue.
- Pharyngeal receptors sense the presence of the bolus and afferent fibers of cranial nerves V, IX and X carry this information to the medulla.
- From this point on, the swallowing reflex is involuntary.



Deglutition (swallowing)

- The medulla coordinates the rest of the swallowing reflex.
- Respiration efforts are inhibited by the medulla, reducing the danger of food inhalation.
- Efferent motor neurons carried by cranial nerves VII, IX, X and XII carry out the following steps.
- Snakes have an interesting adaptation that allows them to take minutes to hours to swallow their meal. In addition to unhinging their jaw to swallow objects many times wider than they are, snakes can extend their glottis and trachea forward and out the side of the mouth. This allows them to take in air during the entire swallowing process.



The enteric nervous system

- The enteric nervous system (ENS) functions from esophagus to anus.
- It consists of two layers of nerve cell bodies named on the basis of their location.
- The cell bodies of the **submucosal plexus (Meissner's plexus)** lie within the submucosa below the tunica mucosa.
- The cell bodies of the **myenteric plexus (Auerbach's plexus)** lie between the inner circular smooth muscle layer that stretches around the circumference of the intestine and the outer longitudinal smooth muscle cells that runs parallel the length of the intestine.
- These nerve cell bodies extend sensory fibers to the secretory, absorptive, and enteroendocrine cells lining the lumen of the gut, as well as sensory fibers within the lamina propria, submucosa, and muscle layers.
- These sensory neurons can detect a variety of changes within the gut, including distension (stretch receptors), pH of the luminal contents, osmolarity, and even the presence of certain toxins.
- These sensory neurons can then relay that information to other neurons within the submucosal or myenteric plexus which may in turn activate efferent neurons within the submucosal and myenteric nerve plexuses to respond to the detected change.

The Brain in Your Gut

The gut's brain, known as the enteric nervous system, is located in sheaths of tissue lining the esophagus, stomach, small intestine and colon.

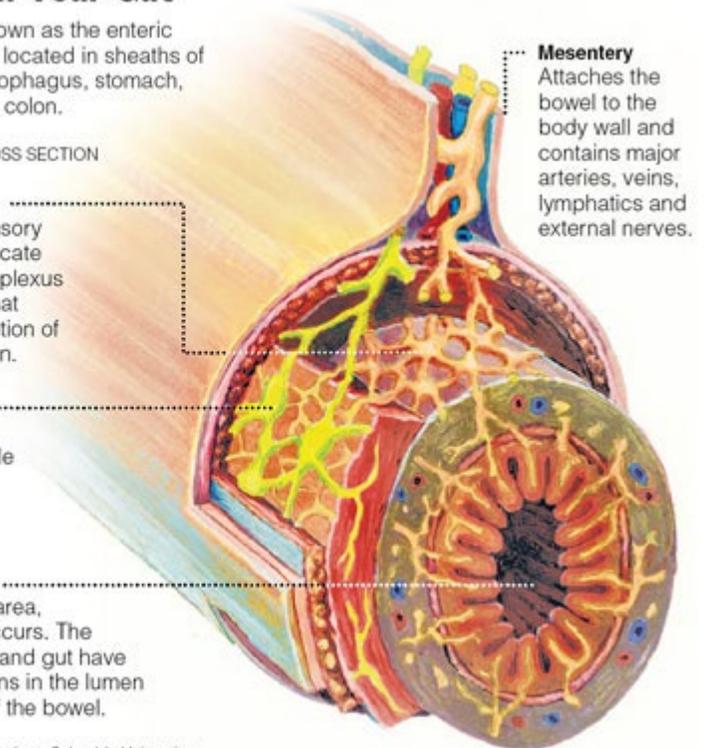
SMALL INTESTINE CROSS SECTION

Submucosal plexus
Layer contains sensory cells that communicate with the myenteric plexus and motor fibers that stimulate the secretion of fluids into the lumen.

Myenteric plexus
Layer contains the neurons responsible for regulating the enzyme output of adjacent organs.

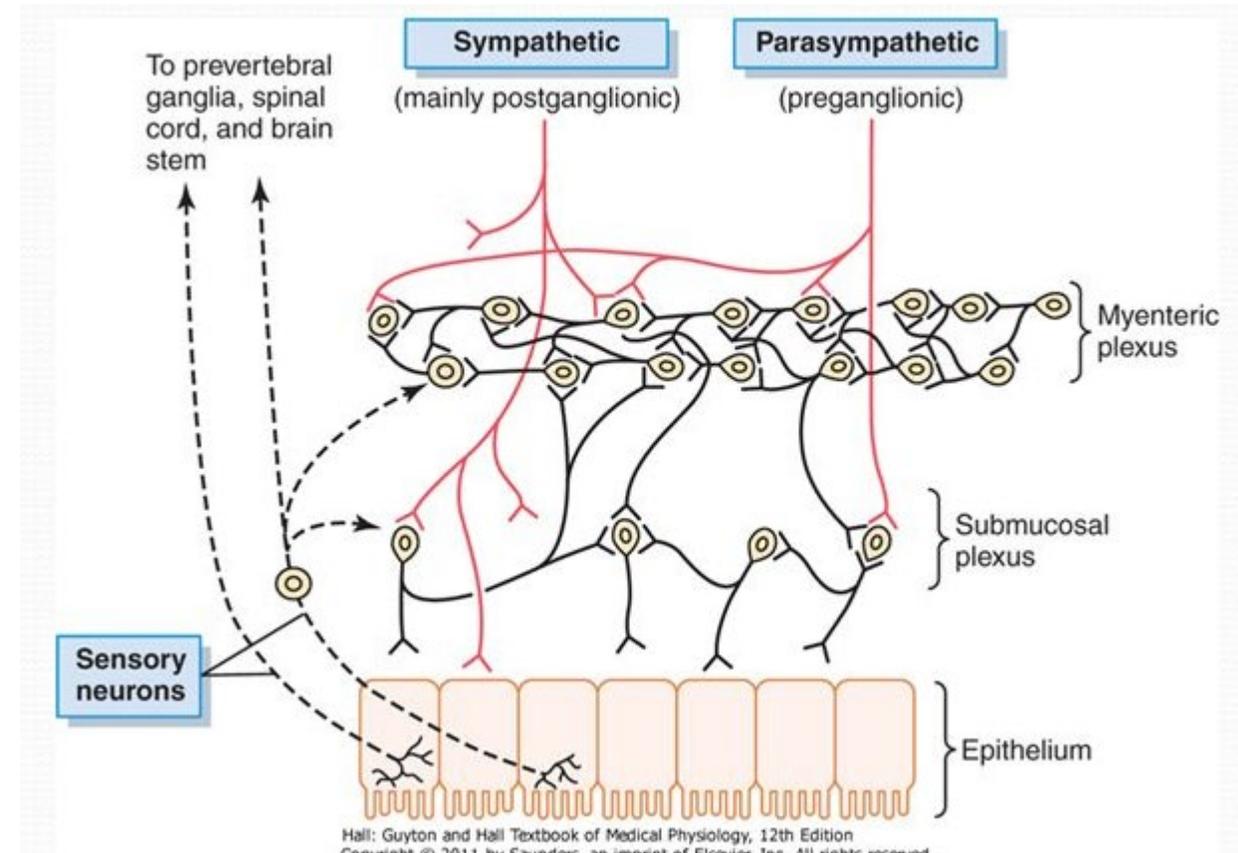
Lumen No nerves
actually enter this area, where digestion occurs. The brains in the head and gut have to monitor conditions in the lumen across the lining of the bowel.

Source: Dr. Michael D. Gershon, Columbia University



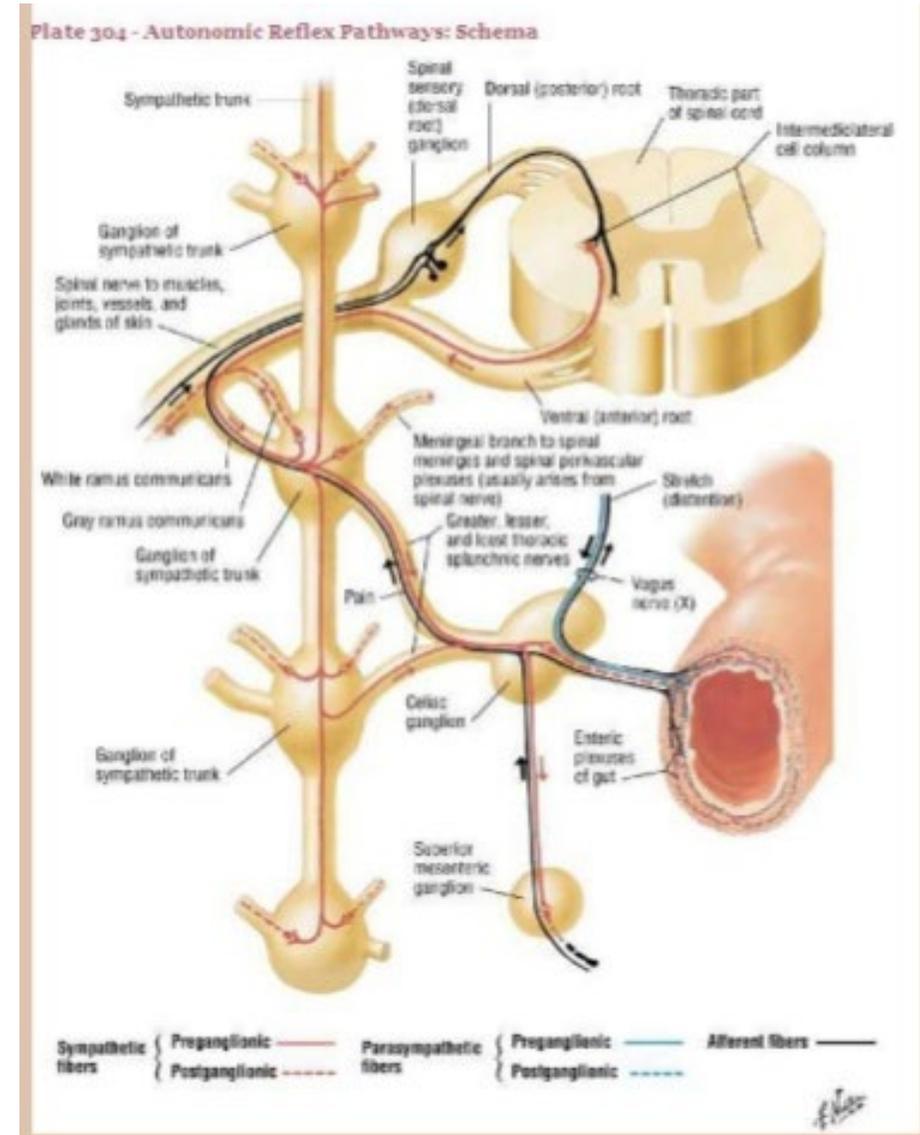
The enteric nervous system

- The efferent neurons of the ENS can secrete a wide variety of neurotransmitters to interact with receptors on their target cells.
- These include acetylcholine, norepinephrine, dopamine, serotonin, and at least 30 other neurotransmitters and bioactive substances such as gastrointestinal peptide, vasoactive intestinal peptide (VIP), and calcitonin gene-related peptide which have very specific actions within the gastrointestinal tract.
- Some of these actions are stimulatory and some inhibitory.
- Responses modulated by these widely varied transmitters might include contraction of the muscle layers in response to distension, secretion of fluids to neutralize acidity, and secretion of mucus to flush toxins away from an area.



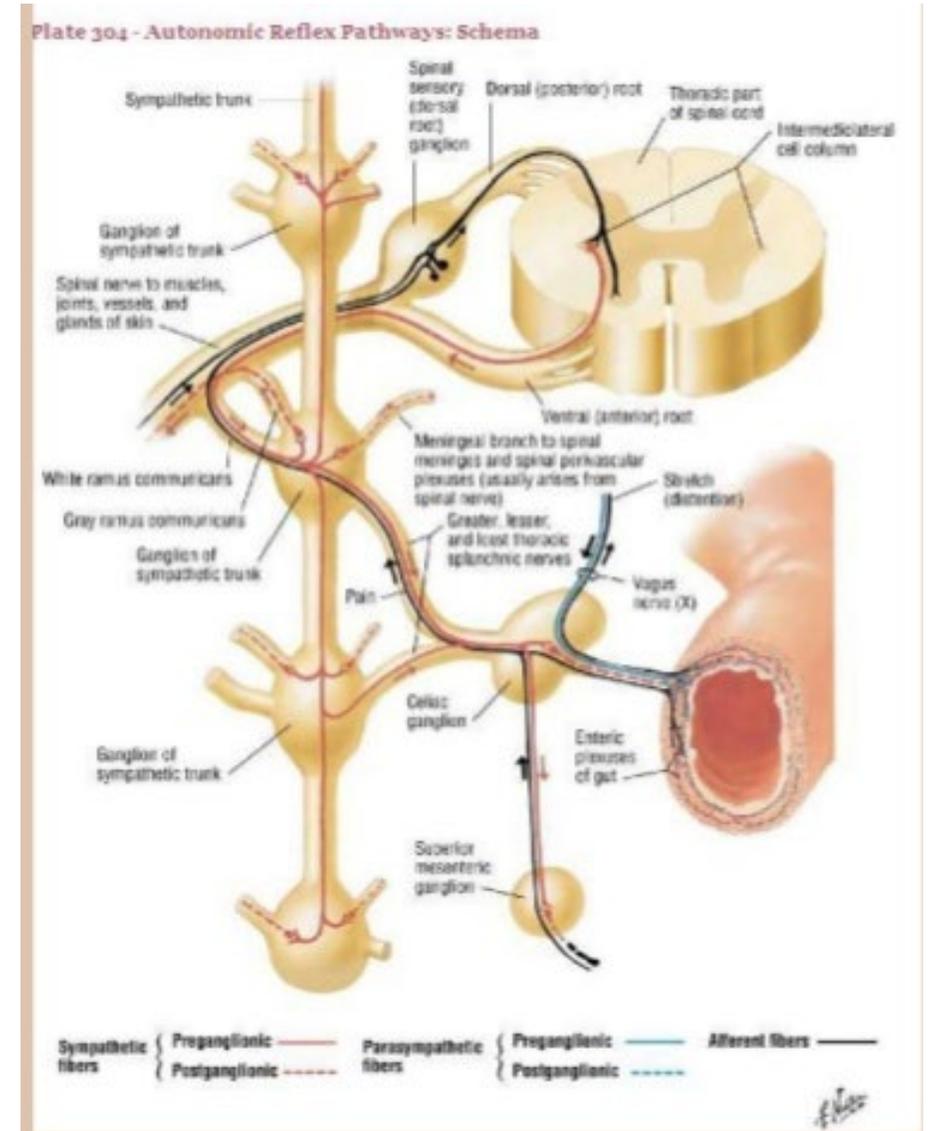
Autonomic Nervous System And The Gastrointestinal Tract

- The efferent parasympathetic system is the predominant player when considering the effects of the autonomic nervous system on the gastrointestinal tract.
- The efferent sympathetic nervous system is often referred to as the “fight or flight” system for its action on heart and respiratory function.
- The parasympathetic system in contrast is referred to as the “rest and digest” system.



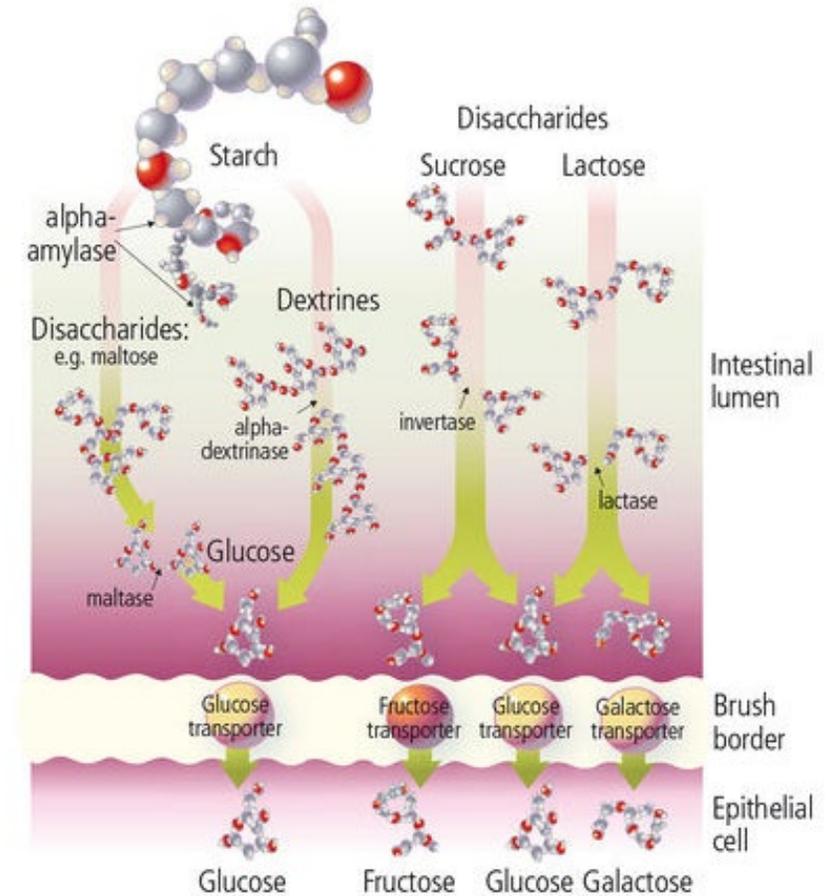
Autonomic Nervous System Summary

- The parasympathetic efferent system is the primary controller of functions associated with motility, secretion, and digestion within the gastrointestinal tract, by directly acting on target cells or by indirectly modulating the activity of the ENS.
- Most of the actions of the gastrointestinal tract are controlled by parasympathetic tone.
- For instance, contraction of the smooth muscles of the outer longitudinal muscle layer increases with increased parasympathetic stimulation or tone and decreases when parasympathetic stimulation is reduced.
- In theory the sympathetic efferent system counteracts the stimulatory actions of the parasympathetic efferent system.
- In practice, the sympathetic efferent action on most functions within the gastrointestinal tract is minor.
- An exception is the effect of the sympathetic efferents on blood flow through the gastrointestinal tract.
- During a “flight or fight” response, the sympathetic efferents quickly shunt blood away from the gastrointestinal tract toward the musculature.



Digestion and Absorption Carbohydrate

- Carbohydrate intake per day ranges from about 250 to 800 g in a typical American diet.
- About two-thirds of this carbohydrate is the plant polysaccharide starch, and most of the remainder consists of the disaccharides sucrose (table sugar) and lactose (milk sugar).
- Only small amounts of monosaccharides are normally present in the diet.
- Cellulose and certain other complex polysaccharides found in vegetable matter—referred to as fiber—cannot be broken down by the enzymes in the small intestine
- They are passed on to the large intestine, where they are partially metabolized by bacteria.



Digestion and Absorption Carbohydrate

- **Starch digestion** by salivary amylase begins in the mouth and continues in the upper part of the stomach before the amylase is destroyed by gastric acid.
- Starch digestion is completed in the small intestine by pancreatic amylase.
- The products produced by both amylases are the disaccharide maltose and a mixture of short, branched chains of glucose molecules.
- These products, along with ingested sucrose and lactose, are broken down into **monosaccharides**—glucose, galactose, and fructose—by enzymes located on the luminal membranes of the small-intestine epithelial cells.
- These monosaccharides are then transported across the intestinal epithelium into the blood.
- Fructose enters the epithelial cells by facilitated diffusion, while glucose and galactose undergo secondary active transport coupled to sodium.
- These monosaccharides then leave the epithelial cells and enter the blood by way of facilitated diffusion transporters in the basolateral membranes of the epithelial cells.
- Most ingested carbohydrate is digested and absorbed within the first 20 percent of the small intestine.

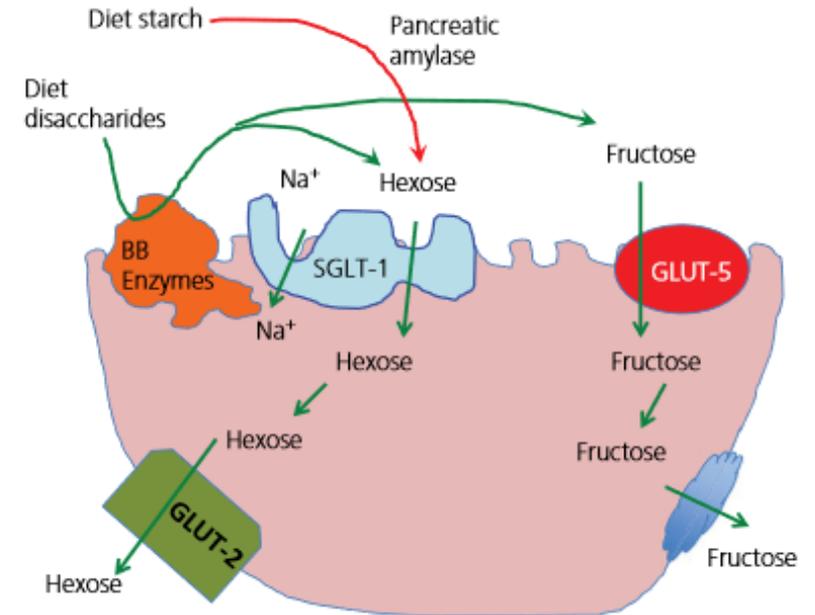
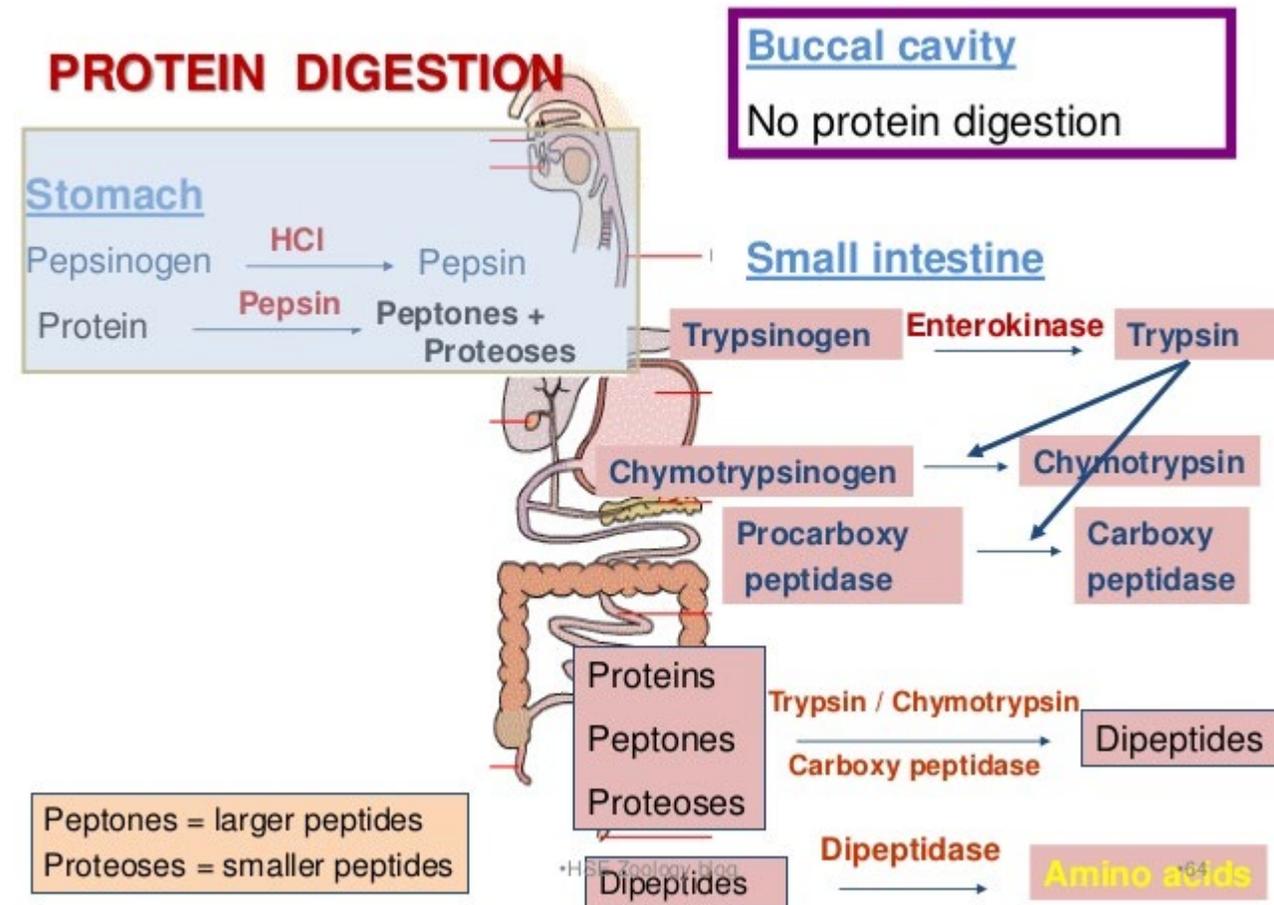


Figure 44.11 Starch is converted to glucose, maltose, and limit dextrins by amylase in the lumen of the intestine. Brush border enzymes (BB enzymes) such as maltase, lactase, sucrase, and dextrinase convert dietary disaccharides (e.g., maltose, lactose, sucrose) and limit dextrins to single hexose (glucose and galactose) or pentose (fructose) molecules. Hexoses in the brush border are brought into the cell using a Na⁺-linked glucose transporter (SGLT-1). Pentose sugars use a Na⁺-independent facilitated transporter (GLUT-5). At the basolateral membrane, both hexose (GLUT-2 transporter) and pentose sugars use facilitated transport diffusion to enter the extracellular fluid down their concentration gradient.

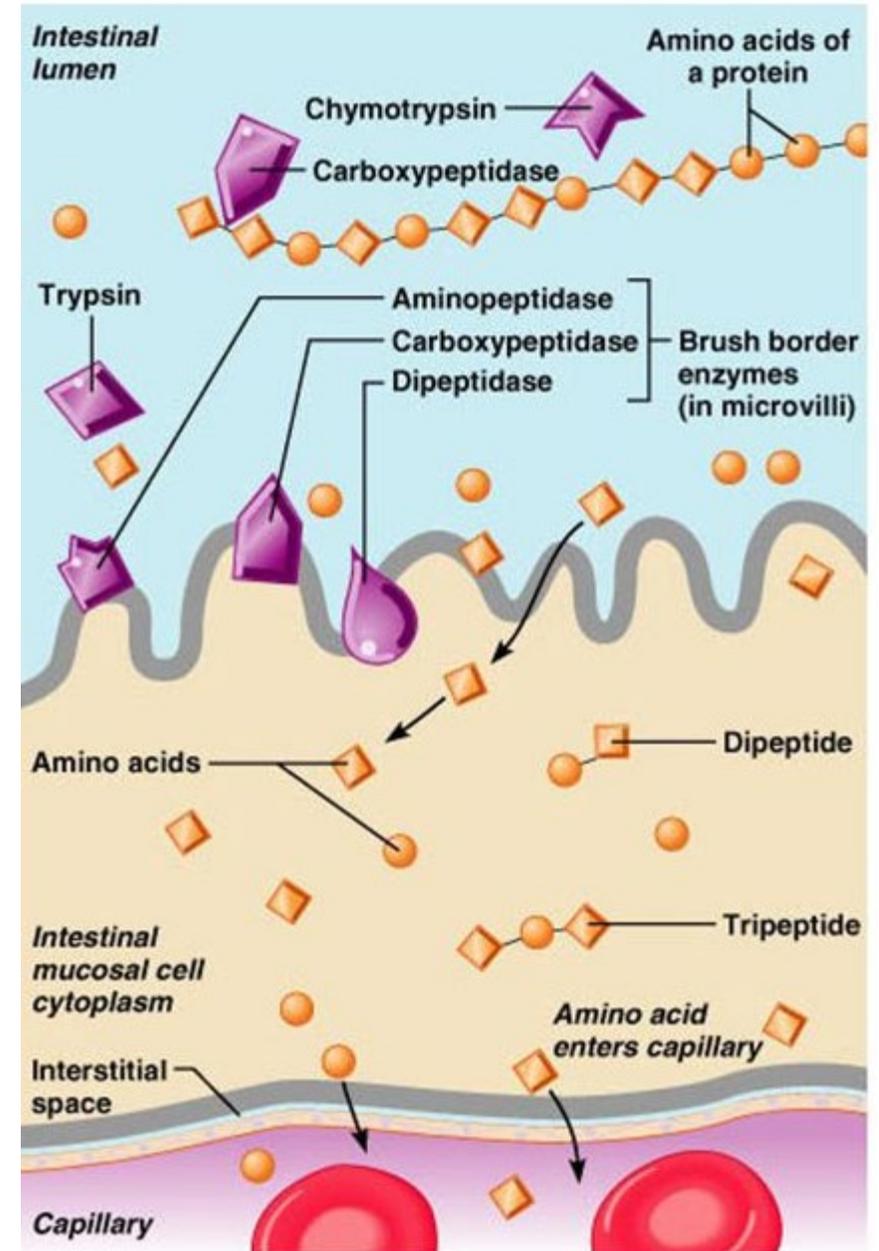
Digestion and Absorption Protein

- Only 40 to 50 g of protein per day is required by a normal adult to supply essential amino acids and replace the amino acid, nitrogen converted to urea.
- In addition, a large amount of protein, in the form of enzymes and mucus, is secreted into the gastrointestinal tract or enters it via the disintegration of epithelial cells.
- Regardless of source, most of the protein in the lumen is broken down into amino acids and absorbed by the small intestine.
- **Proteins** are broken down to **peptide fragments** in the stomach by pepsin, and in the small intestine by trypsin and chymotrypsin, the major proteases secreted by the pancreas.



Digestion and Absorption Protein

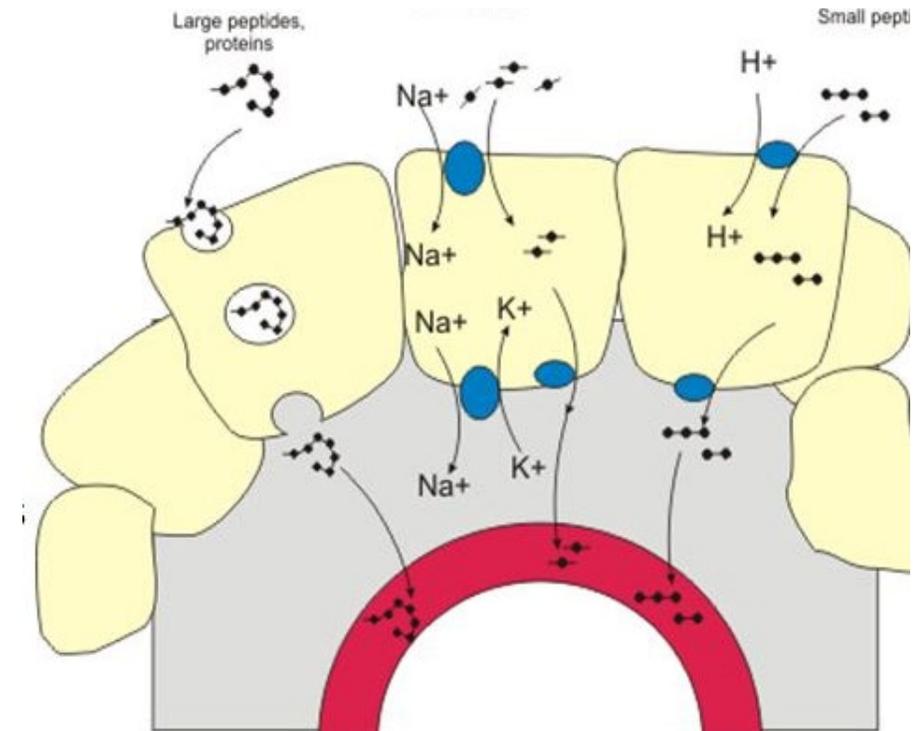
- These fragments are further digested to free amino acids by carboxypeptidase from the **pancreas** and aminopeptidase, located on the luminal membranes of the **small-intestine epithelial cells**.
- These last two enzymes split off amino acids from the carboxyl and amino ends of peptide chains, respectively.
- The free amino acids then enter the epithelial cells by secondary active transport coupled to sodium.
- **Within the epithelial cell, these di- and tripeptides are hydrolyzed to amino acids**, which then leave the cell and enter the blood through a facilitated diffusion carrier in the basolateral membranes.
- As with carbohydrates, protein digestion and absorption are largely completed in the upper portion of the small intestine.



Digestion and Absorption

Protein

- Very small amounts of intact proteins are able to cross the intestinal epithelium and gain access to the interstitial fluid.
- They do so by a combination of endocytosis and exocytosis.
- The absorptive capacity for intact proteins is much greater in infants than in adults, and **antibodies (proteins involved in the immunological defense system of the body) secreted into the mother's milk can be absorbed by the infant**, providing some immunity until the infant begins to produce its own antibodies.



Digestion and Absorption

Fat

- Fat intake ranges from about 25 to 160 g/day in a typical American diet; most is in the form of triacylglycerols.
- Fat digestion occurs almost entirely in the small intestine.
- The major digestive enzyme in this process is **pancreatic lipase**, which catalyzes the splitting of bonds linking fatty acids to the first and third carbon atoms of glycerol, producing **two free fatty acids and a monoglyceride** as products.
- The fats in the ingested foods are insoluble in water and **aggregate into large lipid droplets in the upper portion of the stomach.**

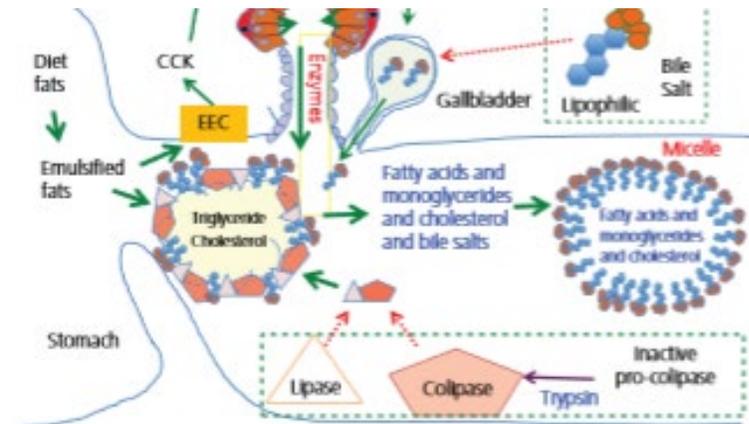
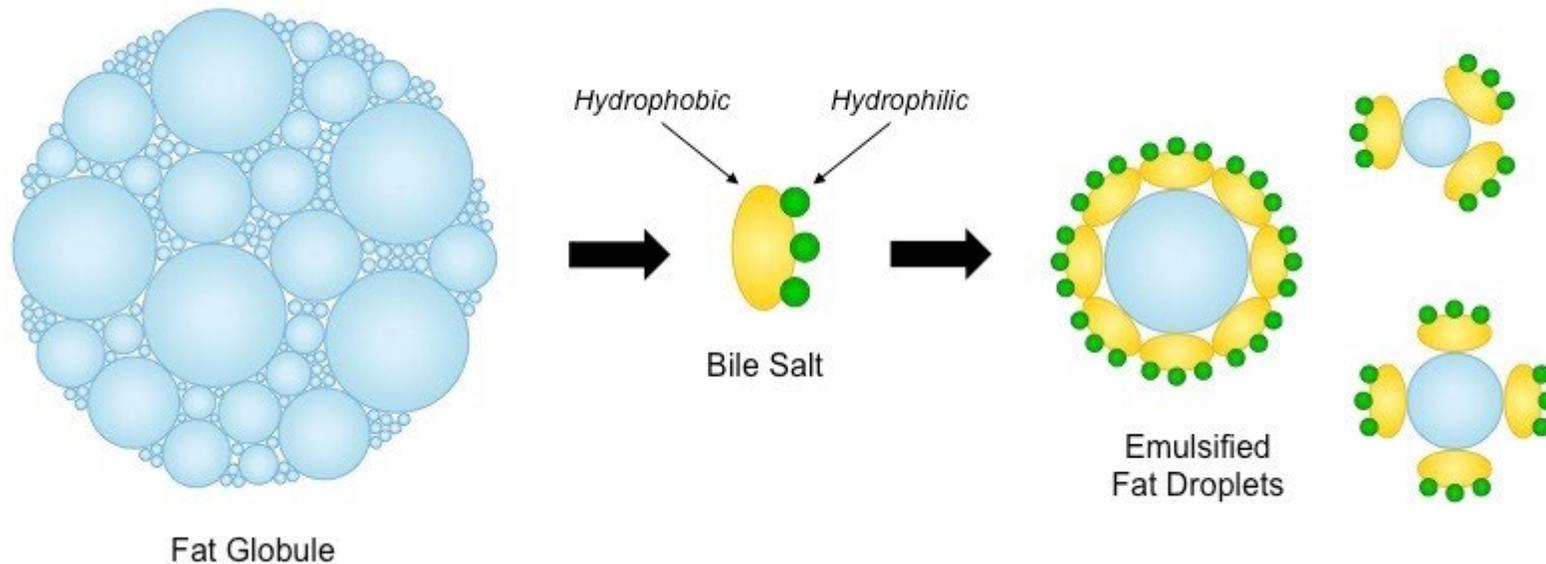


Figure 44.12 Luminal phase of fat digestion. Churning of the stomach emulsifies dietary lipids. As these fats enter the duodenum they stimulate enteroendocrine cells (EEC) to secrete cholecystokinin (CCK). CCK stimulates the pancreas to release digestive enzymes including lipase and pro-colipase needed for fat digestion. CCK also stimulates the gallbladder to contract causing secretion of bile salts into the lumen. Pro-colipase is cleaved by trypsin to form active colipase, which is a cofactor needed for full activity of lipase. Lipase, colipase, and the bile salts work together on the emulsified fat to convert the triglycerides to monoglycerides and free fatty acids. The liberated fatty acids and monoglycerides, as well as cholesterol and fat-soluble vitamins, are surrounded by bile salts to form micelles. Micelles are several hundred fold smaller than the emulsified fat droplet.

Digestion and Absorption

Fat

- Since **pancreatic lipase is a water-soluble enzyme**, its digestive action in the small intestine can take place only at the surface of a lipid droplet.
- Therefore, if most of the ingested fat remained in large lipid droplets, the rate of lipid digestion would be very slow.
- The rate of digestion is, however, substantially increased by division of the large lipid droplets into a number of much smaller droplets, each about 1 mm in diameter, thereby increasing their surface area and accessibility to lipase action.
- This process is known as **emulsification**, and the resulting suspension of small lipid droplets is an emulsion.



Digestion and Absorption

Fat

- **The emulsification of fat requires:**
 - (1) **mechanical disruption of the large fat droplets into smaller droplets, and**
 - (2) **an emulsifying agent, which acts to prevent the smaller droplets from reaggregating back into large droplets.**
- The mechanical disruption is provided by contractile activity, occurring in the lower portion of the stomach and in the small intestine, which acts to grind and mix the luminal contents.
- Phospholipids in food and phospholipids and bile salts secreted in the bile provide the emulsifying agents, whose action is as follows:
 - Phospholipids are amphipathic molecules consisting of two nonpolar fatty acid chains attached to glycerol, with a charged phosphate group located on glycerol's third carbon.
 - Bile salts are formed from cholesterol in the liver and are also amphipathic.
 - The nonpolar portions of the phospholipids and bile salts associate with the nonpolar interior of the lipid droplets, leaving the polar portions exposed at the water surface.
 - There they repel other lipid droplets that are similarly coated with these emulsifying agents, thereby preventing their reaggregation into larger fat droplet

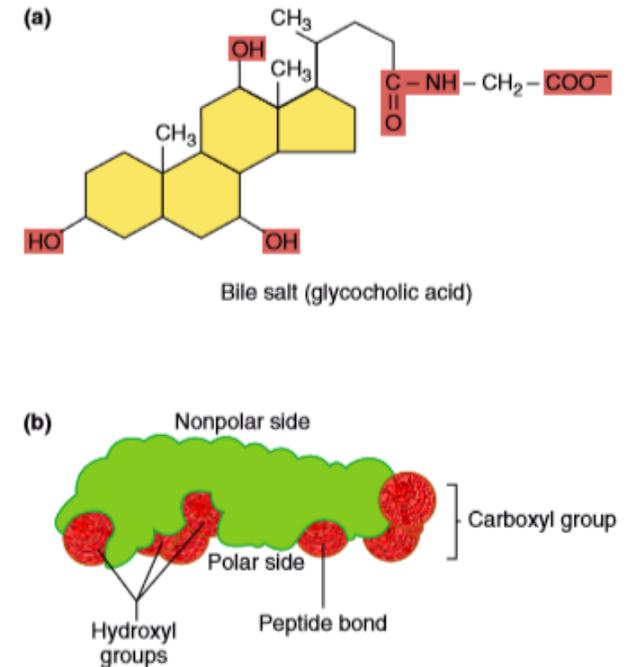


FIGURE 17-9
Structure of bile salts. (a) Chemical formula of glycocholic acid, one of several bile salts secreted by the liver (polar groups in color). (b) Three-dimensional structure of a bile salt, showing its polar and nonpolar surfaces.

Digestion and Absorption

Fat

- The coating of the lipid droplets with these emulsifying agents impairs the accessibility of the water-soluble lipase to its lipid substrate.
- To overcome this problem, the pancreas secretes a protein known as **colipase**, which is amphipathic and lodges on the lipid droplet surface.
- Colipase binds the lipase enzyme, holding it on the surface of the lipid droplet.
- **Although digestion is speeded up by emulsification, absorption of the water-insoluble products of the lipase reaction would still be very slow if it were not for a second action of the bile salts, the formation of micelles,** which are similar in structure to emulsion droplets but are much smaller—4 to 7 nm in diameter.
- Micelles consist of **bile salts, fatty acids, monoglycerides,** and **phospholipids** all clustered together with the polar ends of each molecule oriented toward the micelle's surface and the nonpolar portions forming the micelle's core.
- Also included in the core of the micelle are small amounts of **fatsoluble vitamins** and cholesterol.

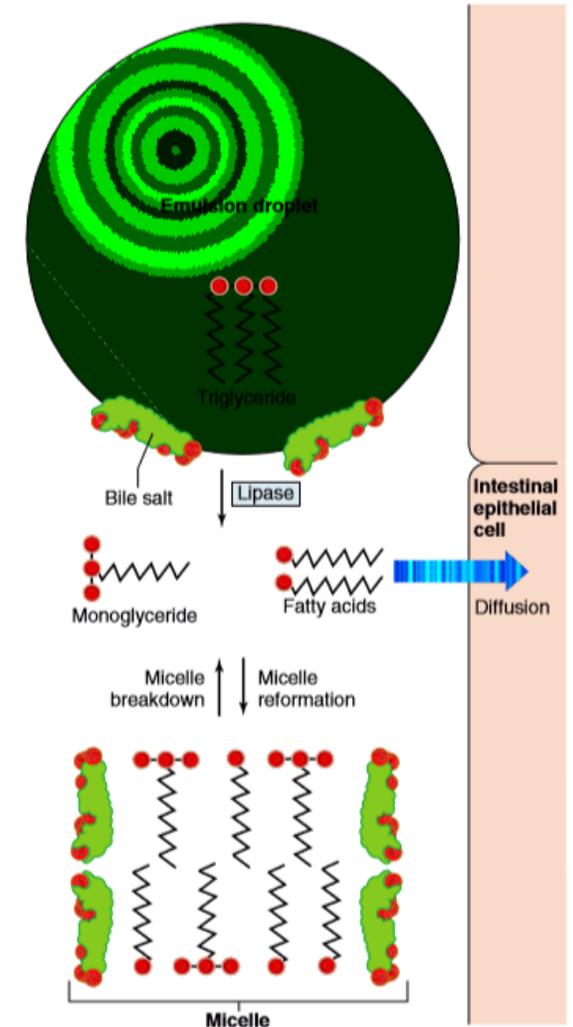


FIGURE 17-11

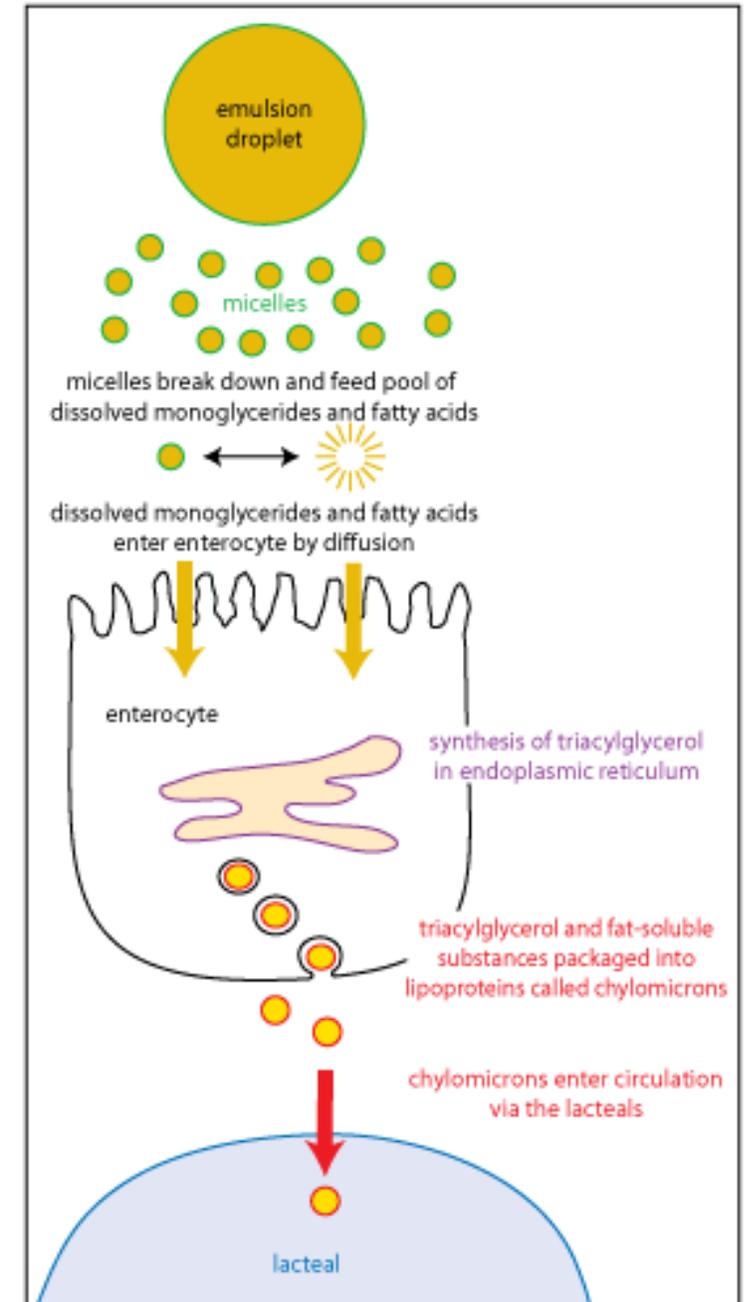
The products of fat digestion by lipase are held in solution in the micellar state, combined with bile salts and phospholipids. For simplicity, the phospholipids and colipase (see text) are not shown and the size of the micelle is greatly exaggerated. 

Digestion and Absorption

Fat

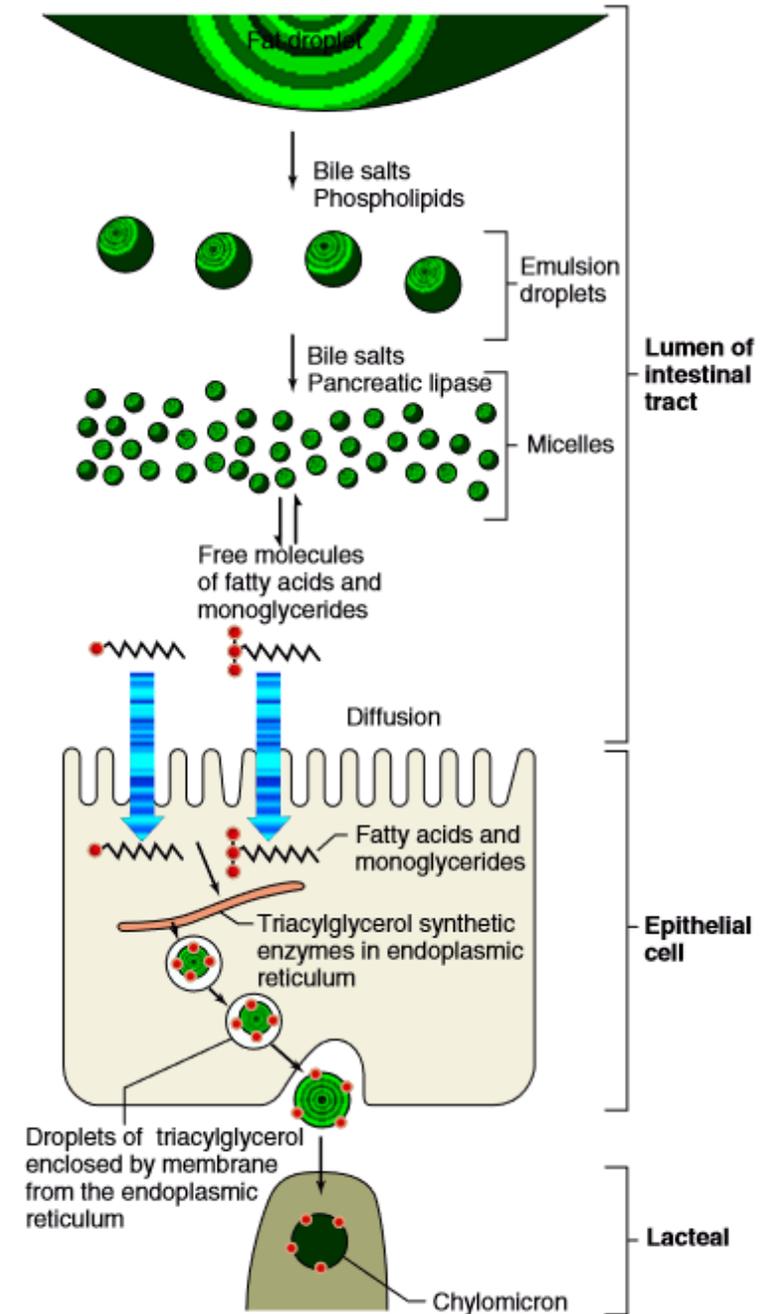
- **How do micelles increase absorption?**

- Micelles, containing the products of fat digestion, are in equilibrium with the small concentration of fat digestion products that are free in solution.
- Thus, micelles are continuously breaking down and reforming.
- When a micelle breaks down, its contents are released into the solution and become available to diffuse across the intestinal lining.
- **As the concentrations of free lipids fall, because of their diffusion into epithelial cells, more lipids are released into the free phase as micelles break down.**
- Thus, the micelles provide a means of keeping most of the insoluble fat digestion products in small soluble aggregates, while at the same time replenishing the small amount of products that are free in solution and are able to diffuse into the intestinal epithelium.
- **Note that it is not the micelle that is absorbed but rather the individual lipid molecules that are released from the micelle.**



Fat Digestion and Absorption

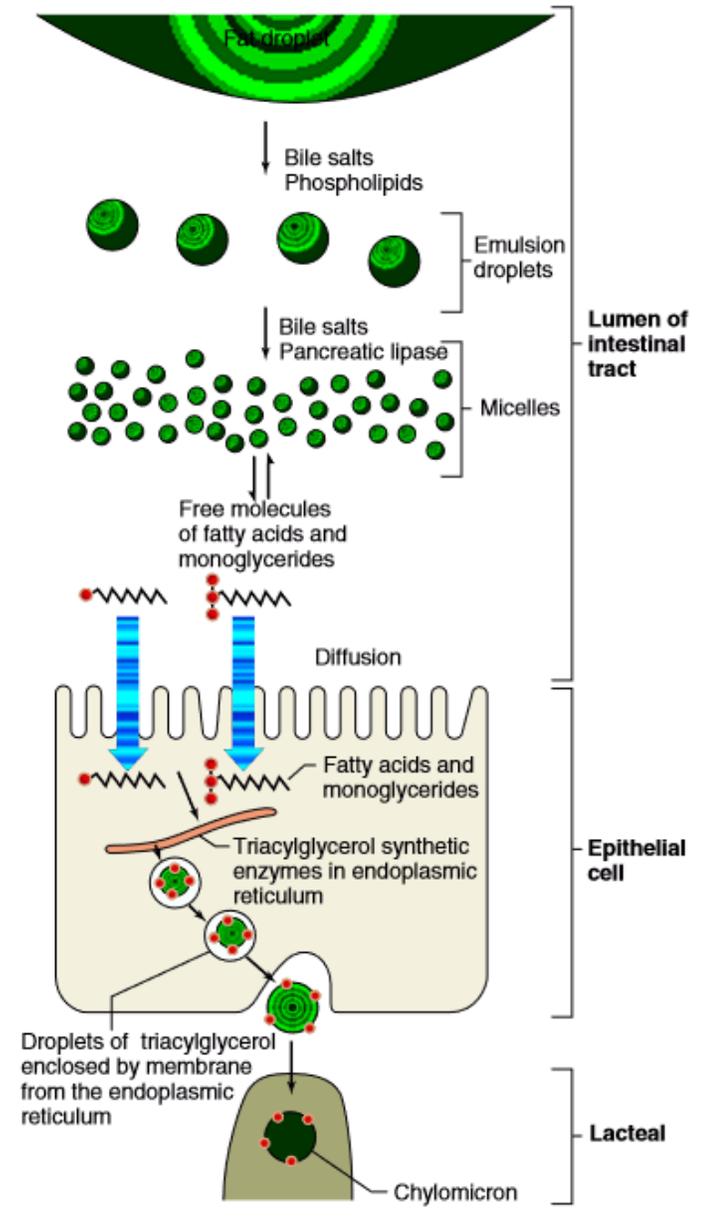
- During their passage through the epithelial cells, fatty acids and monoglycerides are resynthesized into **triacylglycerols**.
- This occurs in the agranular (smooth) **endoplasmic reticulum**, where the enzymes for triacylglycerol synthesis are located.
- **This process lowers the concentration of cytosolic free fatty acids and monoglycerides and thus maintains a diffusion gradient for these molecules into the cell.**
- Within this organelle, the resynthesized fat aggregates into small droplets coated with amphipathic proteins that perform an emulsifying function similar to that of bile salts.
- The exit of these fat droplets from the cell follows the same pathway as a secreted protein.
- Vesicles containing the droplet pinch off the endoplasmic reticulum, are processed through the Golgi apparatus, and eventually fuse with the plasma membrane, releasing the fat droplet into the interstitial fluid.



Digestion and Absorption

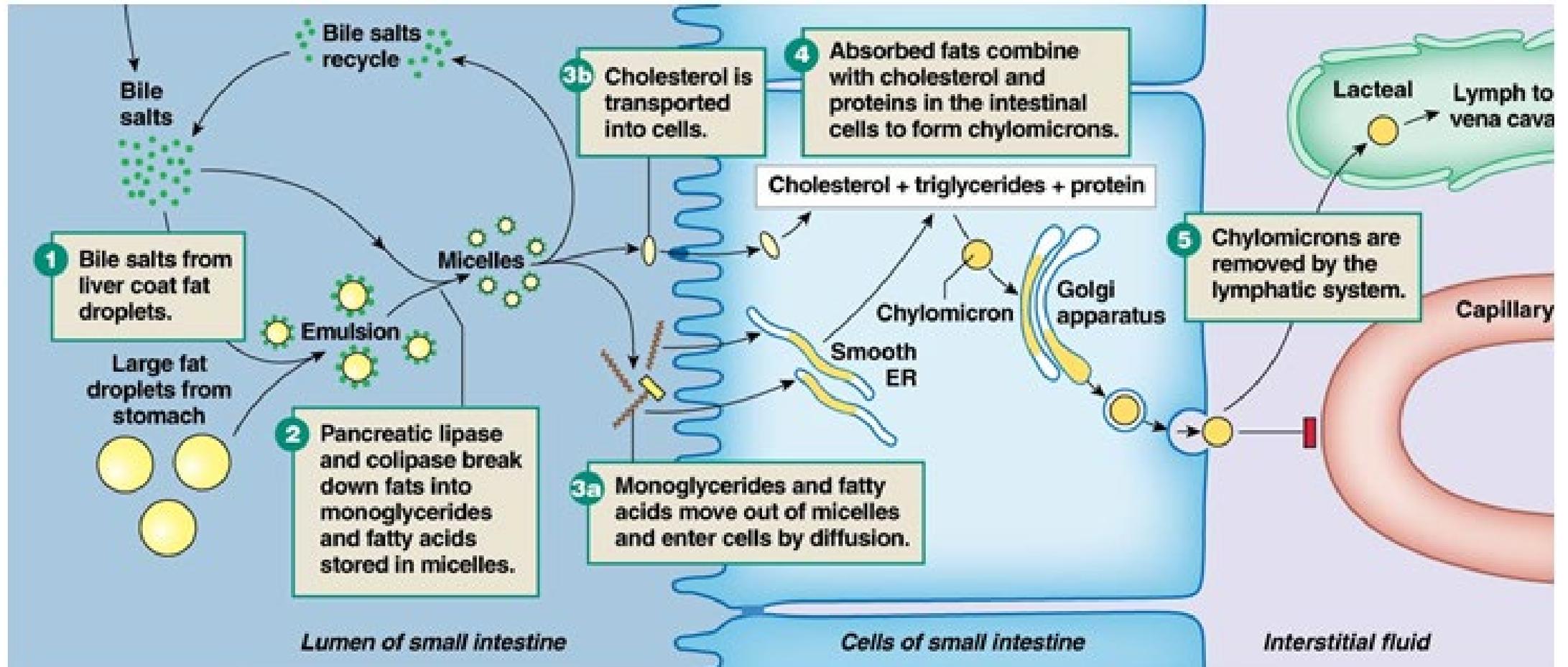
Fat

- These onem micron-diameter, extracellular fat droplets are known as **chylomicrons**.
- Chylomicrons contain not only triacylglycerols but other lipids (including phospholipids, cholesterol, and fat-soluble vitamins) that have been absorbed by the same process that led to fatty acid and monoglyceride movement into the epithelial cells of the small intestine.
- The chylomicrons released from the epithelial cells pass into lacteals—lymphatic capillaries in the intestinal villi.
- The chylomicrons cannot enter the blood capillaries because the basement membrane at the outer surface of the capillary provides a barrier to the diffusion of large chylomicrons.
- In contrast, the lacteals do not have basement membranes and have large slit pores between their endothelial cells through which the chylomicrons can pass into the lymph.
- The lymph from the small intestine, as from everywhere else in the body, eventually empties into systemic veins.



Digestion and Absorption

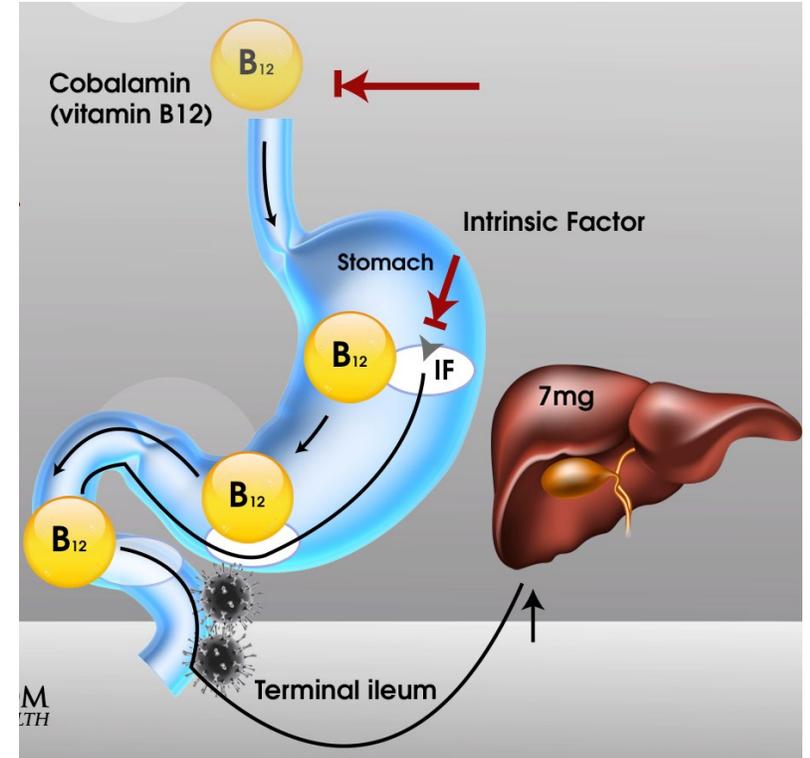
Fat



Digestion and Absorption

Vitamins

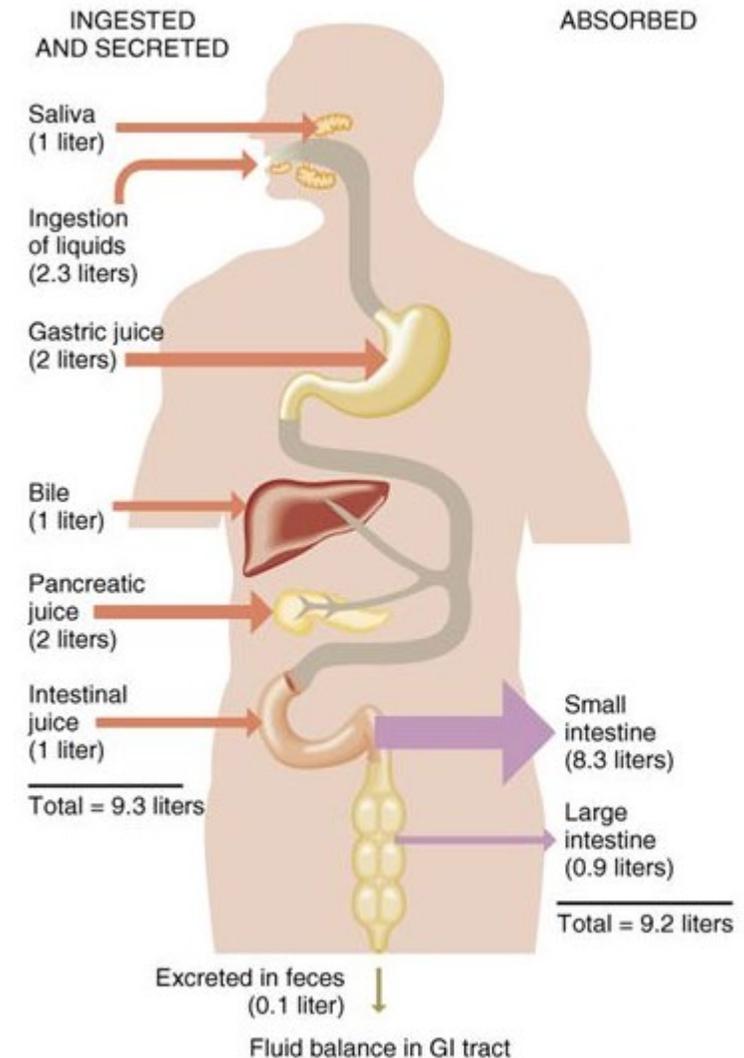
- The fat-soluble vitamins—A, D, E, and K—follow the pathway for fat absorption described in the previous section.
- They are solubilized in micelles.
- With one exception, water-soluble vitamins are absorbed by diffusion or mediated transport.
- The exception, vitamin B12, is a very large, charged molecule.
- **In order to be absorbed, vitamin B12 must first bind to a protein, known as intrinsic factor, secreted by the acid secreting cells in the stomach.**
- Intrinsic factor with bound vitamin B12 then binds to specific sites on the epithelial cells in the lower portion of the ileum, where **vitamin B12 is absorbed by endocytosis**



Digestion and Absorption

Water and Minerals

- Water is the most abundant substance in chyme.
- Approximately 8000 ml of ingested and secreted water enters the small intestine each day, but only 1500 ml is passed on to the large intestine since 80 percent of the fluid is absorbed in the small intestine.
- Small amounts of water are absorbed in the stomach, but the stomach has a much smaller surface area available for diffusion and lacks the solute-absorbing mechanisms that create the osmotic gradients necessary for net water absorption.
- The epithelial membranes of the small intestine are very permeable to water, and net water diffusion occurs across the epithelium whenever a water concentration difference is established by the active absorption of solutes.



Digestion and Absorption

Iron

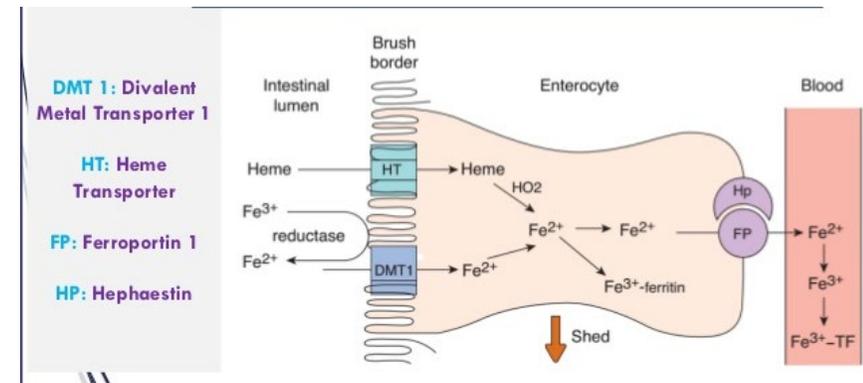
- Once iron has entered the blood, the body has very little means of excreting it, **and it accumulates in tissues.**
- Although the control mechanisms for iron absorption tend to maintain the iron content of the body fairly constant, a very large ingestion of iron can overwhelm them, leading to an increased deposition of iron in tissues and producing toxic effects.
- This condition is termed **hemochromatosis.**
- Iron absorption also depends on the type of food ingested because it binds to many negatively charged ions in food, which can retard its absorption.
- For example, iron in ingested liver is much more absorbable than iron in egg yolk since the latter contains phosphates that bind the iron to form an insoluble and unabsorbable complex.
- The absorption of iron is typical of that of most trace metals in several respects:
 - (1) Cellular storage proteins and plasma carrier proteins are involved, and
 - (2) the control of absorption, rather than urinary excretion, is the major mechanism for the homeostatic control of the body's content of the trace metal.



Digestion and Absorption

Iron

- Only about 10 percent of ingested iron is absorbed into the blood each day.
- Iron ions are actively transported into intestinal epithelial cells, where most of them are incorporated into **ferritin**, *the protein-iron complex that functions as an intracellular iron store*.
- The absorbed iron that does not bind to ferritin is released on the blood side where it circulates throughout the body bound to the plasma protein **transferrin**.
- Most of the iron bound to ferritin in the epithelial cells is released back into the intestinal lumen when the cells at the tips of the villi disintegrate, and it is excreted in the feces.
- **Iron absorption depends on the body's iron content.** When body stores are ample, the increased concentration of free iron in the plasma and intestinal epithelial cells leads to an increased transcription of the gene encoding the ferritin protein and thus an increased synthesis of ferritin.
- **When the body stores drop, for example, when there is a loss of hemoglobin during hemorrhage, the production and hence the concentration of intestinal ferritin decreases; the amount of iron bound to ferritin decreases, thereby increasing the unbind iron released in the body.**



Regulation of Gastrointestinal Processes

- Basic Principles Gastrointestinal reflexes are initiated by a relatively small number of luminal stimuli:
 - (1) distension of the wall by the volume of the luminal contents;
 - (2) chyme osmolarity (total solute concentration);
 - (3) chyme acidity; and
 - (4) chyme concentrations of specific digestion products (monosaccharides, fatty acids, peptides, and amino acids).
- These stimuli act on receptors located in the wall of the tract (mechanoreceptors, osmoreceptors, and chemoreceptors) to trigger reflexes that influence the effectors—the muscle layers in the wall of the tract and the exocrine glands that secrete substances into its lumen.

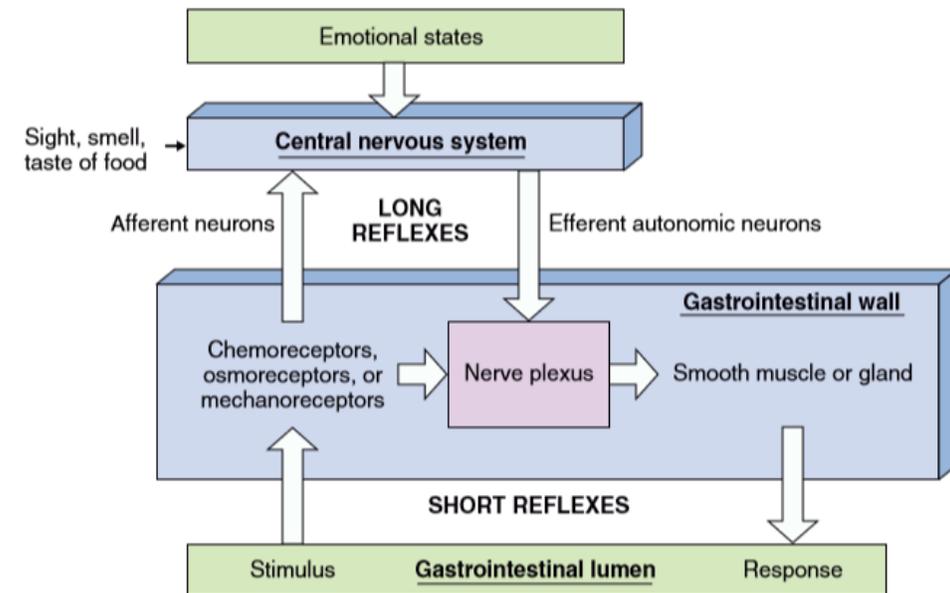
Neural Regulation

- The gastrointestinal tract has its own local nervous system, known as the **enteric nervous system**, in the form of two nerve networks, the **myenteric plexus** and the **submucous plexus**.
- Two types of neural reflex arcs exist:
 - (1) short reflexes from receptors through the nerve plexuses to effector cells; and
 - (2) long reflexes from receptors in the tract to the CNS by way of afferent nerves and back to the nerve plexuses and effector cells by way of autonomic nerve fibers.

Some controls are mediated either solely by short reflexes or solely by long reflexes, whereas other controls involve both.

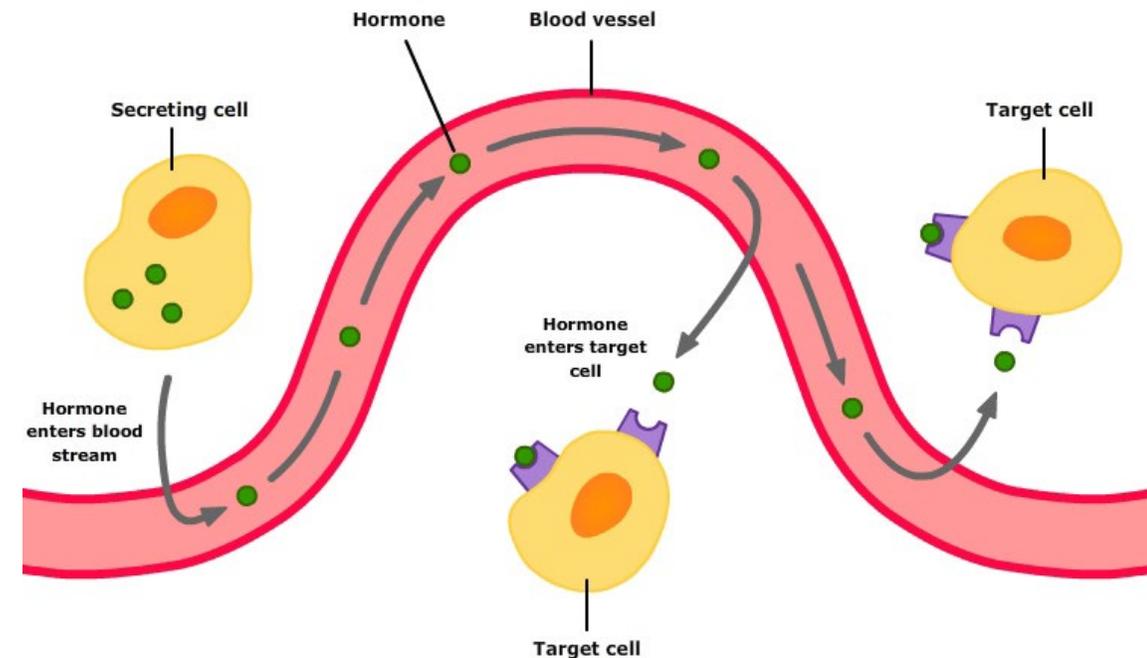
Finally, it should be noted that not all neural reflexes are indicated by signals within the tract.

The sight or smell of food and the emotional state of an individual can have significant effects on the gastrointestinal tract, effects that are mediated by the CNS via autonomic neurons.



Hormonal Regulation

- The hormones that control the gastrointestinal system are secreted mainly by endocrine cells scattered throughout the epithelium of the stomach and small intestine.
- One surface of each endocrine cell is exposed to the lumen of the gastrointestinal tract.
- At this surface, various chemical substances in the chyme stimulate the cell to release its hormones from the opposite side of the cell into the blood.
- Although some of these hormones can also be detected in the lumen and may therefore act locally as paracrine agents, most of the gastrointestinal hormones reach their target cells via the circulation.
- Several dozen substances are currently being investigated as possible gastrointestinal hormones, but only four—**secretin, cholecystinin (CCK), gastrin, and glucose-dependent insulinotropic peptide (GIP)**— have met all the criteria for true hormones.



Hormonal Regulation

- Major characteristics of the four established GI hormones illustrates the following generalizations:
- (1) Each hormone participates in a feedback control system that regulates some aspect of the GI luminal environment, and
- (2) Each hormone affects more than one type of target cell.
- These two generalizations can be illustrated by CCK.
- The presence of fatty acids and amino acids in the small intestine triggers CCK secretion from cells in the small intestine into the blood.
- Circulating CCK then stimulates secretion by the pancreas of digestive enzymes.
- CCK also causes the gallbladder to contract, delivering to the intestine the bile salts required for micelle formation. As fat and amino acids are absorbed, the stimuli (fatty acids and amino acids in the lumen) for CCK release are removed.

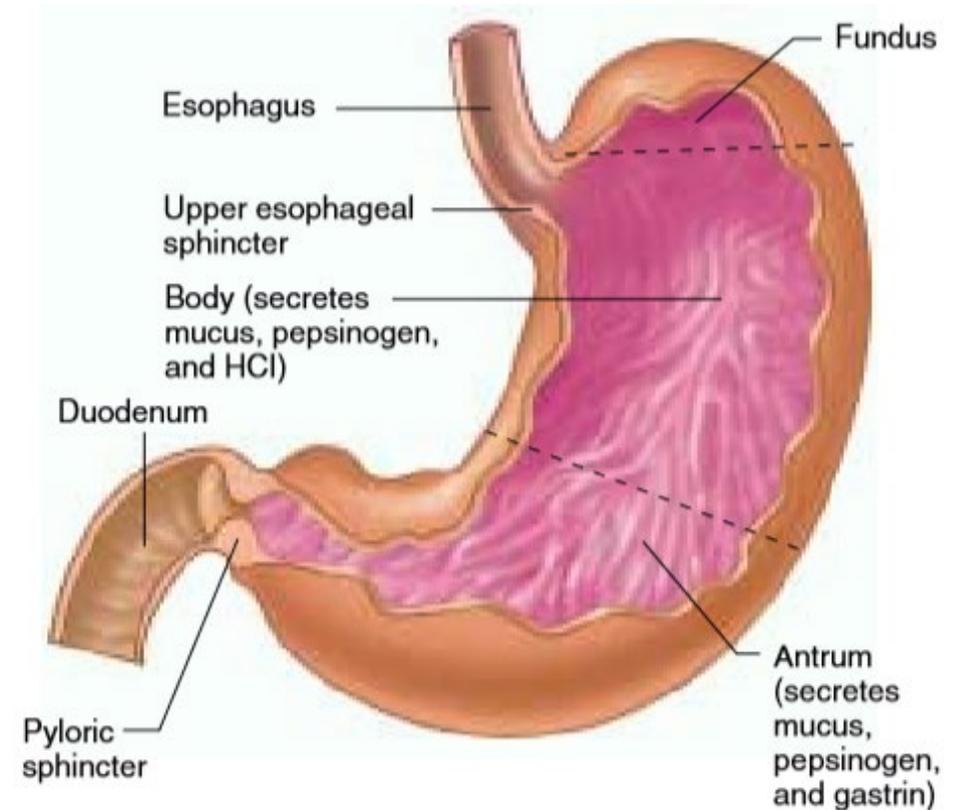
	Gastrin	CCK	Secretin	GIP
Structure	Peptide	Peptide	Peptide	Peptide
Endocrine-Cell location	Antrum of stomach	Small intestine	Small intestine	Small intestine
Stimuli for hormone release	Amino acids, peptides in stomach; parasympathetic nerves	Amino acids, fatty acids in small intestine	Acid in small intestine	Glucose, fat in small intestine
Stimuli inhibiting hormone release	Acid in stomach; somatostatin			

Target-Cell Responses

Stomach				
Acid secretion	Stimulates	Inhibits	Inhibits	
Motility	Stimulates	Inhibits	Inhibits	
Growth	Stimulates			
Pancreas				
Bicarbonate secretion		Potentiates secretin's actions	Stimulates	
Enzyme secretion		Stimulates	Potentiates CCK's actions	
Insulin secretion				Stimulates
Growth of exocrine pancreas	Stimulates	Stimulates	Stimulates	
Liver (bile ducts)				
Bicarbonate secretion		Potentiates secretin's actions	Stimulates	
Gallbladder				
Contraction		Stimulates		
Sphincter of Oddi		Relaxes		
Small intestine				
Motility	Stimulates ileum			
Growth	Stimulates			
Large intestine	Stimulates mass movement			

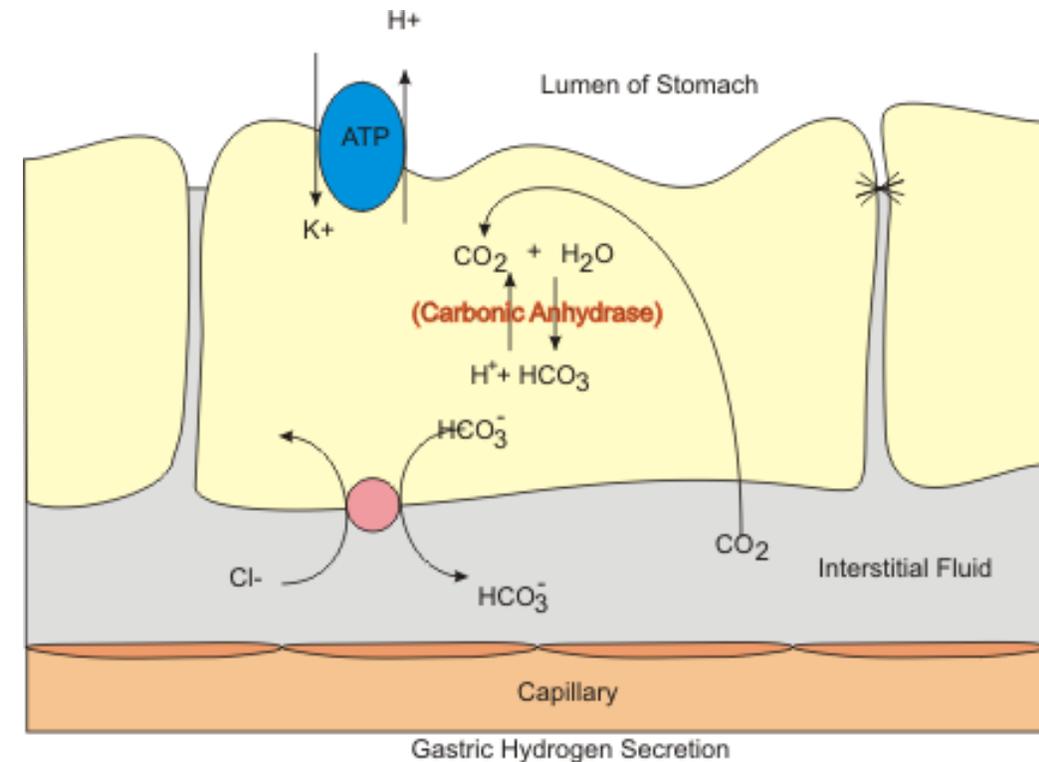
Stomach

- The epithelial layer lining the stomach invaginates into the mucosa, forming numerous tubular glands.
- Glands in the thin-walled upper portions of the stomach, the **body and fundus secrete mucus, hydrochloric acid, and the enzyme precursor pepsinogen.**
- The lower portion of the stomach, the **antrum**, has a much thicker layer of smooth muscle.
- The glands in this region secrete little acid but contain the endocrine cells that secrete the hormone **gastrin.**
- Mucus is secreted by the cells at the opening of the glands
- Lining the walls of the glands are **parietal cells** (also known as oxyntic cells), which secrete **acid and intrinsic factor**, and **chief cells**, which secrete **pepsinogen.**
- Thus, each of the three major exocrine secretions of the stomach—mucus, acid, and pepsinogen—is secreted by a different cell type.
- In addition, **enterochromaffin-like (ECL) cells**, which release the paracrine agent **histamine**, and cells that secrete the peptide messenger **somatostatin**, are scattered throughout the tubular glands.



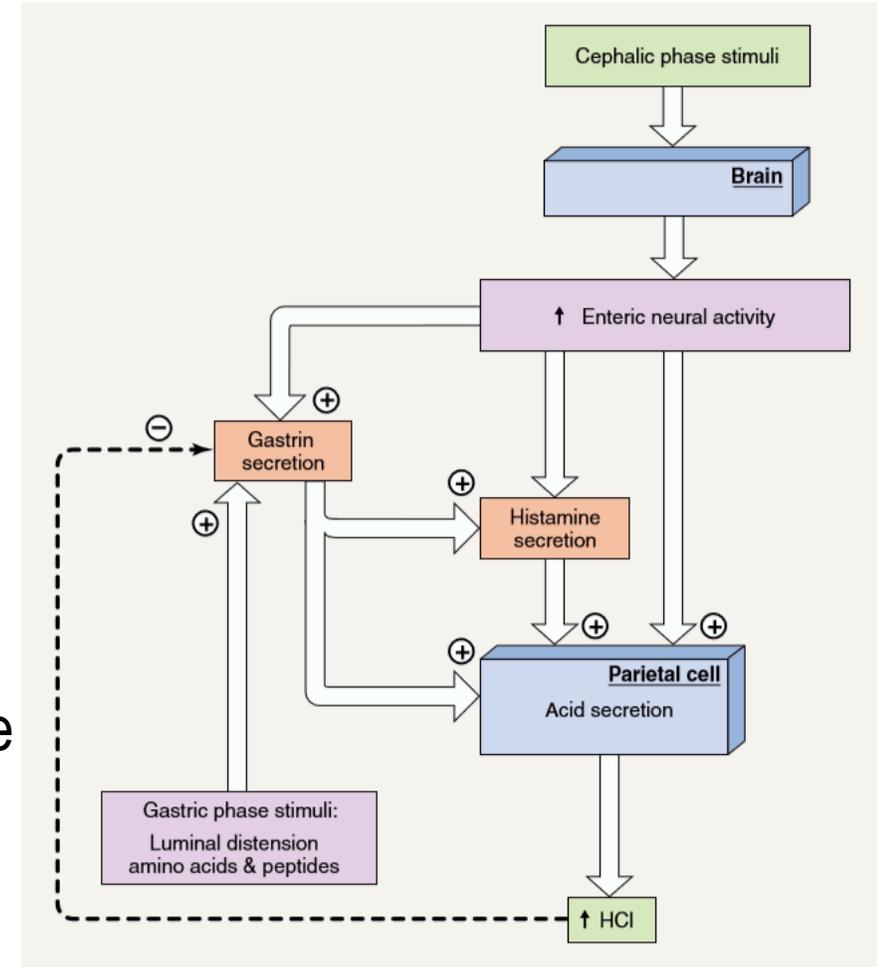
HCl Secretion

- The stomach secretes about 2 L of hydrochloric acid per day.
- The concentration of hydrogen ions in the stomach's lumen may reach 150 mM, 3 million times greater than the concentration in the blood.
- Primary **H,K-ATPases** in the luminal membrane of the parietal cells pump hydrogen ions into the stomach's lumen.
- This primary active transporter also pumps potassium into the cell, which then leaks back into the lumen through potassium channels.
- As hydrogen ions are secreted into the lumen, bicarbonate ions are being secreted on the opposite side of the cell into the blood, in exchange for chloride ions.
- This addition of bicarbonate lowers the acidity in the venous blood from the stomach.



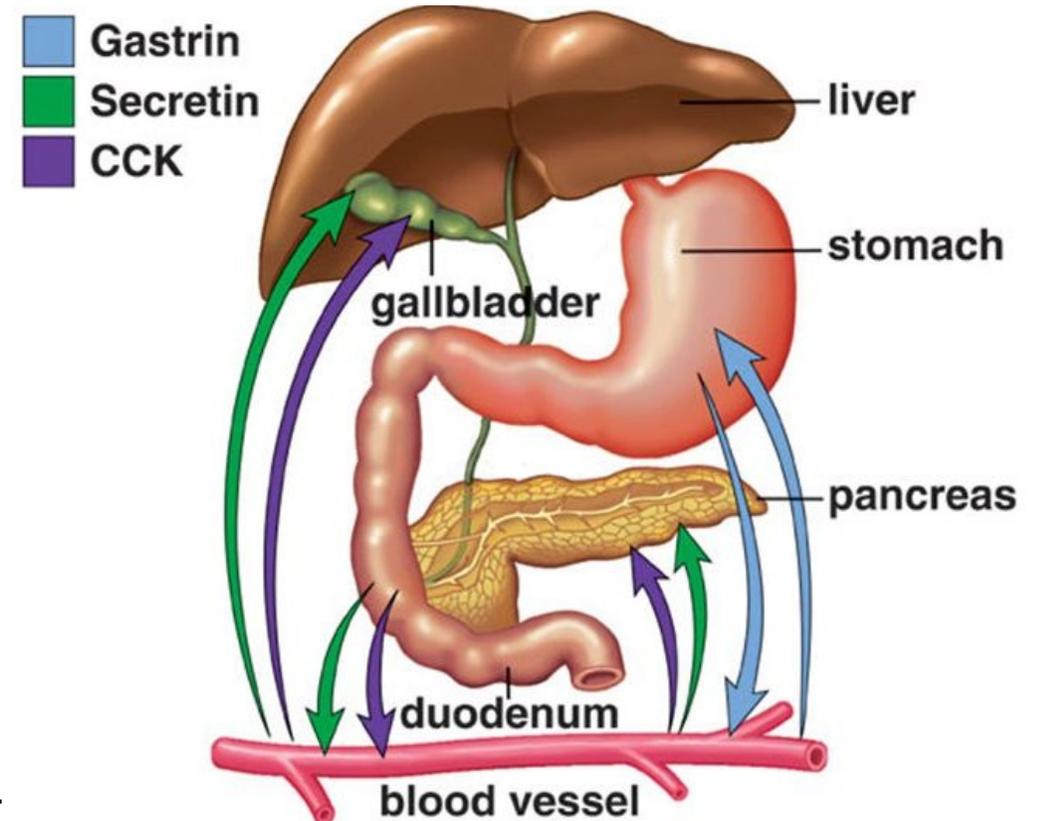
HCl Secretion

- Four chemical messengers regulate the insertion of H,K-ATPases into the plasma membrane and hence acid secretion:
 1. **Gastrin (a GI hormone),**
 2. **Acetylcholine (ACh, a neurotransmitter),**
 3. **Histamine, and**
 4. **Somatostatin (two paracrine agents).**
- Parietal cell membranes contain receptors for all four of these agents.
- **Somatostatin inhibits acid secretion**, while the other three stimulate secretion.
- Histamine is particularly important in stimulating acid secretion in that it markedly potentiates the response to the other two stimuli, gastrin and ACh.



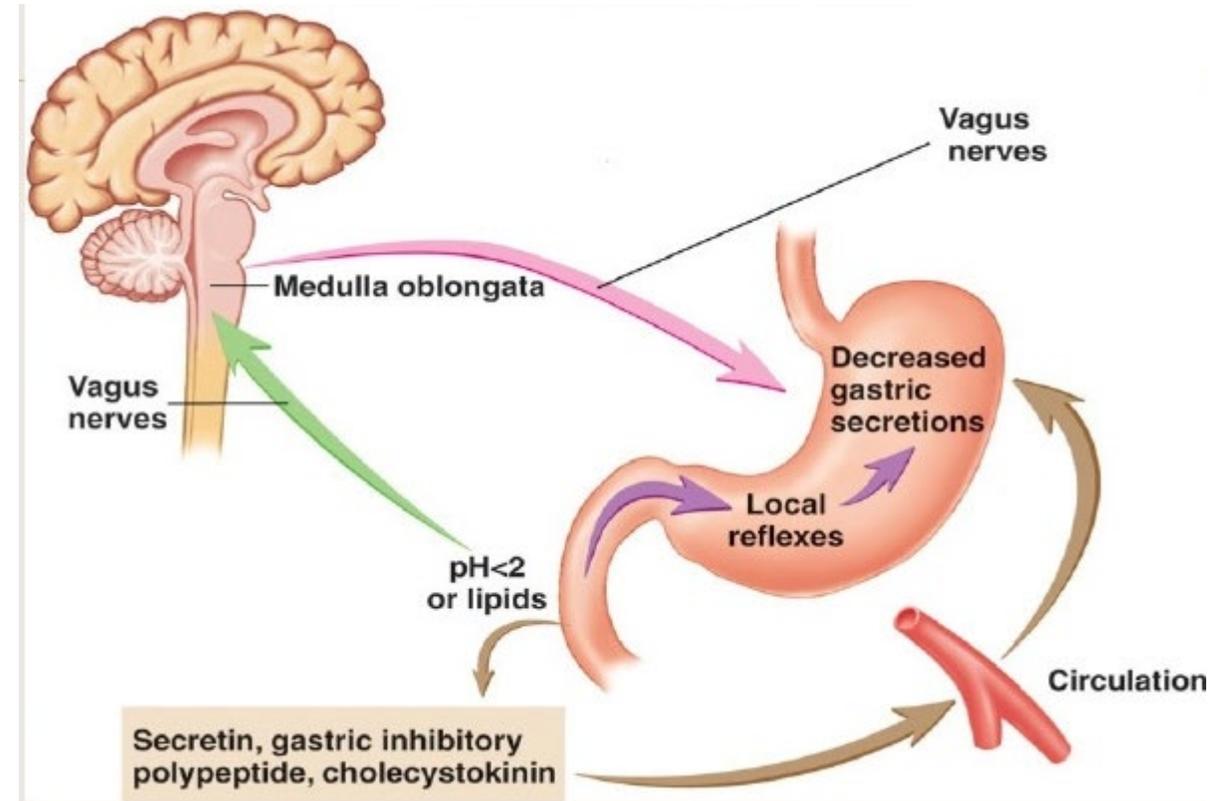
HCl Secretion

- During a meal, the rate of acid secretion increases markedly as stimuli arising from the cephalic, gastric, and intestinal phases alter the release of the four chemical messengers described before.
- In addition, **peptides and amino acids can act directly on the gastrin-releasing endocrine cells to promote gastrin secretion.**
- The concentration of acid in the gastric lumen is itself an important determinant of the rate of acid secretion for the following reason.
- **Hydrogen ions (acid) stimulate the release of somatostatin from endocrine cells in the gastric wall.**
- Somatostatin then acts on the parietal cells to inhibit acid secretion; it also inhibits the release of gastrin and histamine.
- The net result is a negative-feedback control of acid secretion; as the acidity of the gastric lumen increases, it turns off the stimuli that are promoting acid secretion.



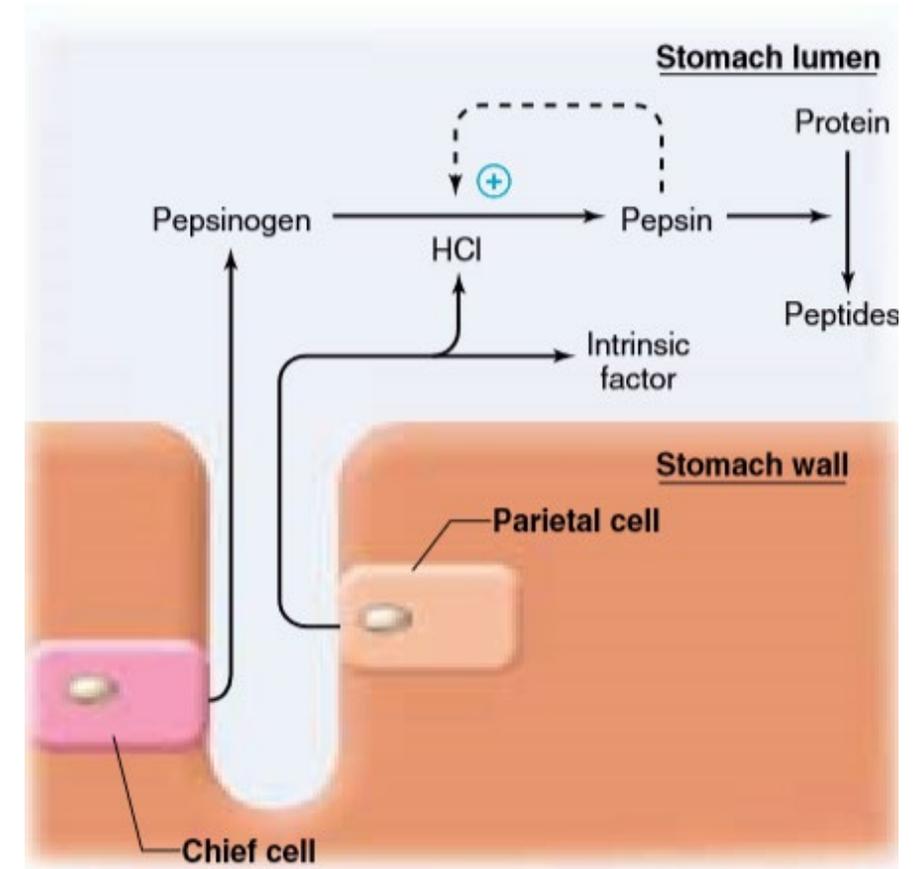
HCl Secretion

- The intestinal phase controlling acid secretion: the phase in which stimuli in the early portion of the small intestine influence acid secretion by the stomach.
- First, high acidity in the duodenum triggers reflexes that inhibit gastric acid secretion.
- This inhibition is beneficial for the following reason:
 - The digestive activity of enzymes and bile salts in the small intestine is strongly inhibited by acidic solutions, and this reflex ensures that acid secretion by the stomach will be reduced whenever chyme entering the small intestine from the stomach contains so much acid that it cannot be rapidly neutralized by the bicarbonate-rich fluids simultaneously secreted into the intestine by the liver and pancreas.
 - Acid, distension, hypertonic solutions, and solutions containing amino acids, and fatty acids in the small intestine reflexly inhibit gastric acid secretion.
 - The inhibition of gastric acid secretion during the intestinal phase is mediated by short and long neural reflexes and by hormones.
 - The hormones released by the intestinal tract that reflexly inhibit gastric activity are collectively called **enterogastrones** and include **secretin**, **CCK**, and additional unidentified hormones.



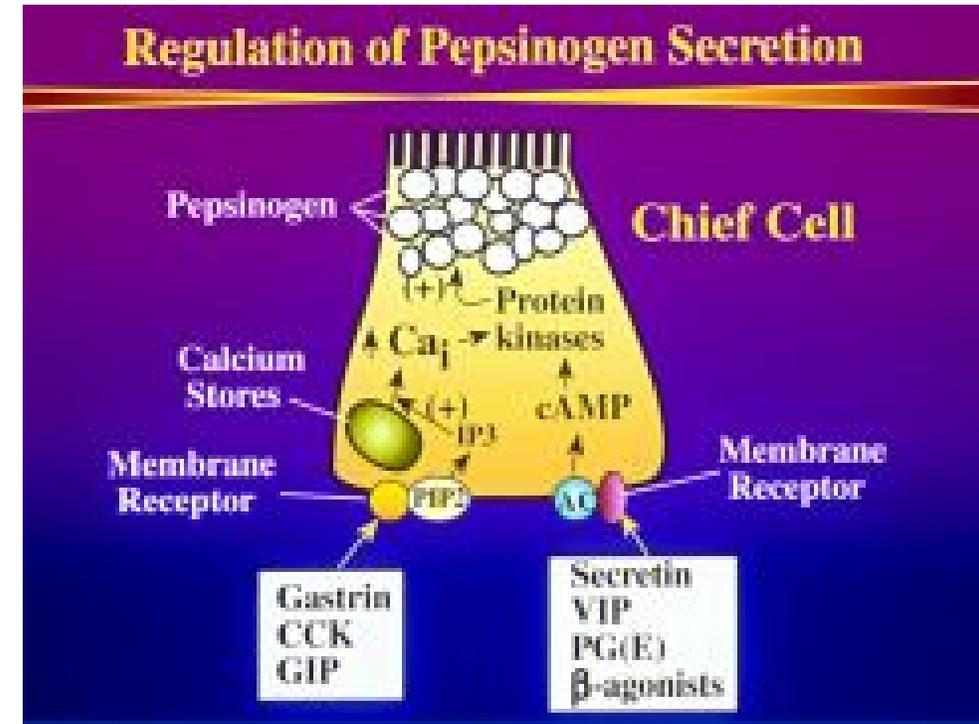
Pepsin Secretion

- Pepsin is secreted by chief cells in the form of an inactive precursor called **pepsinogen**.
- The acidity in the stomach's lumen alters the shape of pepsinogen, exposing its active site so that this site can act on other pepsinogen molecules to break off a small chain of amino acids from their ends.
- This cleavage converts **pepsinogen to pepsin**, the fully active form.
- Thus the activation of pepsin is an autocatalytic, positive-feedback process.
- The synthesis and secretion of pepsinogen, followed by its intraluminal activation to pepsin, provides an example of a process that occurs with many other secreted proteolytic enzymes in the gastrointestinal tract.
- Because these enzymes are synthesized in inactive forms, collectively referred to as **zymogens**, any substrates that these enzymes might be able to act upon inside the cell producing them are protected from digestion, thus preventing damage to the cells.



Pepsin Secretion

- Pepsin is active only in the presence of a high H concentration.
- **It becomes inactive when it enters the small intestine, where the hydrogen ions are neutralized by the bicarbonate ions secreted into the small intestine.**
- The primary pathway for stimulating pepsinogen secretion is input to the chief cells from the enteric nervous system.
- During the cephalic, gastric, and intestinal phases, most of the factors that stimulate or inhibit acid secretion exert the same effect on pepsinogen secretion.
- Thus, pepsinogen secretion parallels acid secretion.
- **Pepsin is not essential for protein digestion since in its absence, as occurs in some pathological conditions, protein can be completely digested by enzymes**



Gastric Motility

- An empty stomach has a volume of only about 50 ml, and the diameter of its lumen is only slightly larger than that of the small intestine.
- When a meal is swallowed, however, the smooth muscles in the fundus and body relax before the arrival of food, allowing the stomach's volume to increase to as much as 1.5 L with little increase in pressure.
- This is called **receptive relaxation** and is mediated by the parasympathetic nerves to the stomach's enteric nerve plexuses, with coordination by the swallowing center in the brain.
- Nitric oxide and serotonin released by enteric neurons mediate this relaxation.

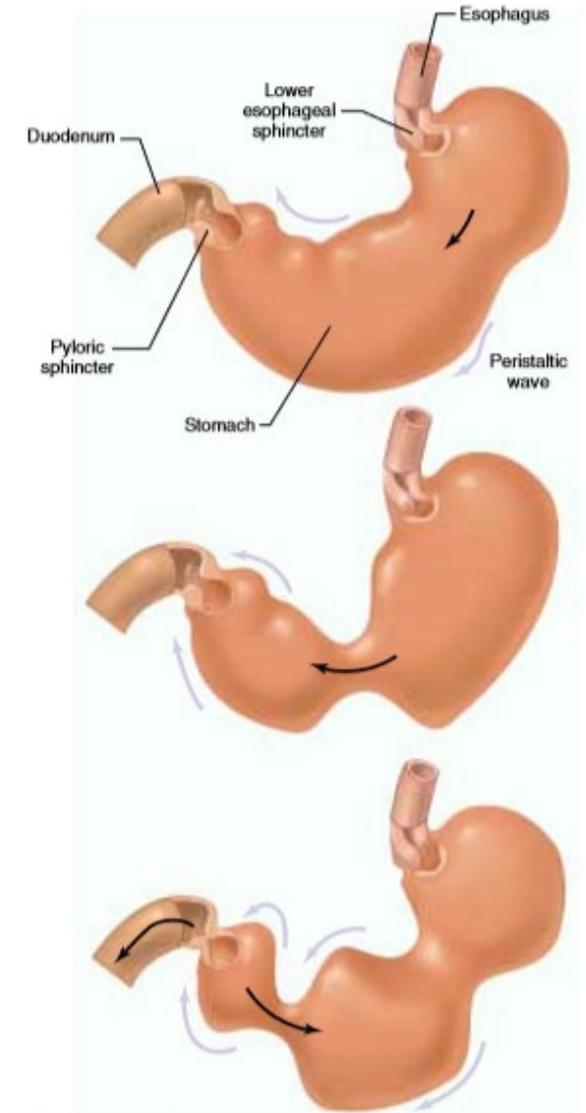


FIGURE 17-22
Peristaltic waves passing over the stomach force a small amount of luminal material into the duodenum. Black arrows indicate movement of luminal material; purple arrows indicate movement of the peristaltic wave in the stomach wall. 

Gastric Motility

- As in the esophagus, **the stomach produces peristaltic waves** in response to the arriving food.
- **Each wave begins in the body of the stomach** and produces only a ripple as it proceeds toward the antrum, a contraction too weak to produce much mixing of the luminal contents with acid and pepsin.
- **As the wave approaches the larger mass of wall muscle surrounding the antrum, it produces a more powerful contraction, which both mixes the luminal contents and closes the pyloric sphincter, a ring of smooth muscle and connective tissue between the antrum and the duodenum.**
- The pyloric sphincter muscles contract upon arrival of a peristaltic wave.
- As a consequence of sphincter closing, **only a small amount of chyme is expelled into the duodenum with each wave, and most of the antral contents are forced backward toward the body of the stomach, thereby contributing to the mixing activity in the antrum.**

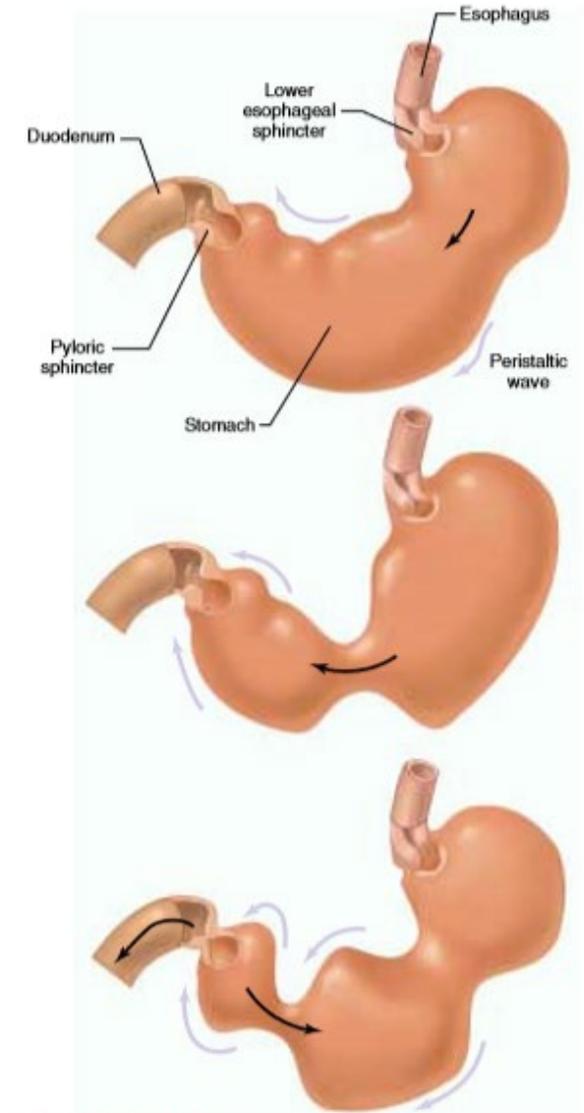
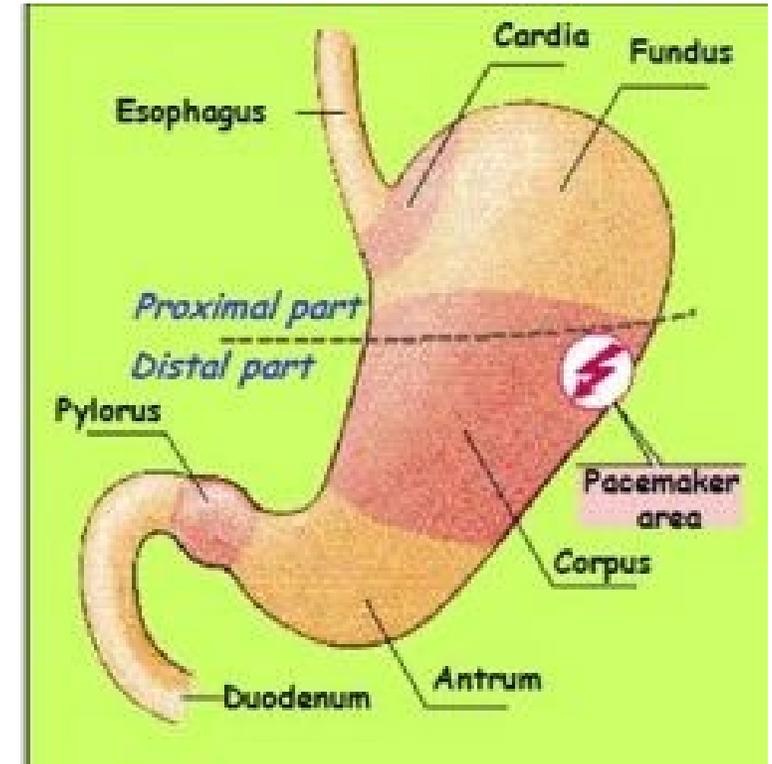


FIGURE 17-22
Peristaltic waves passing over the stomach force a small amount of luminal material into the duodenum. Black arrows indicate movement of luminal material; purple arrows indicate movement of the peristaltic wave in the stomach wall. 

Gastric Motility

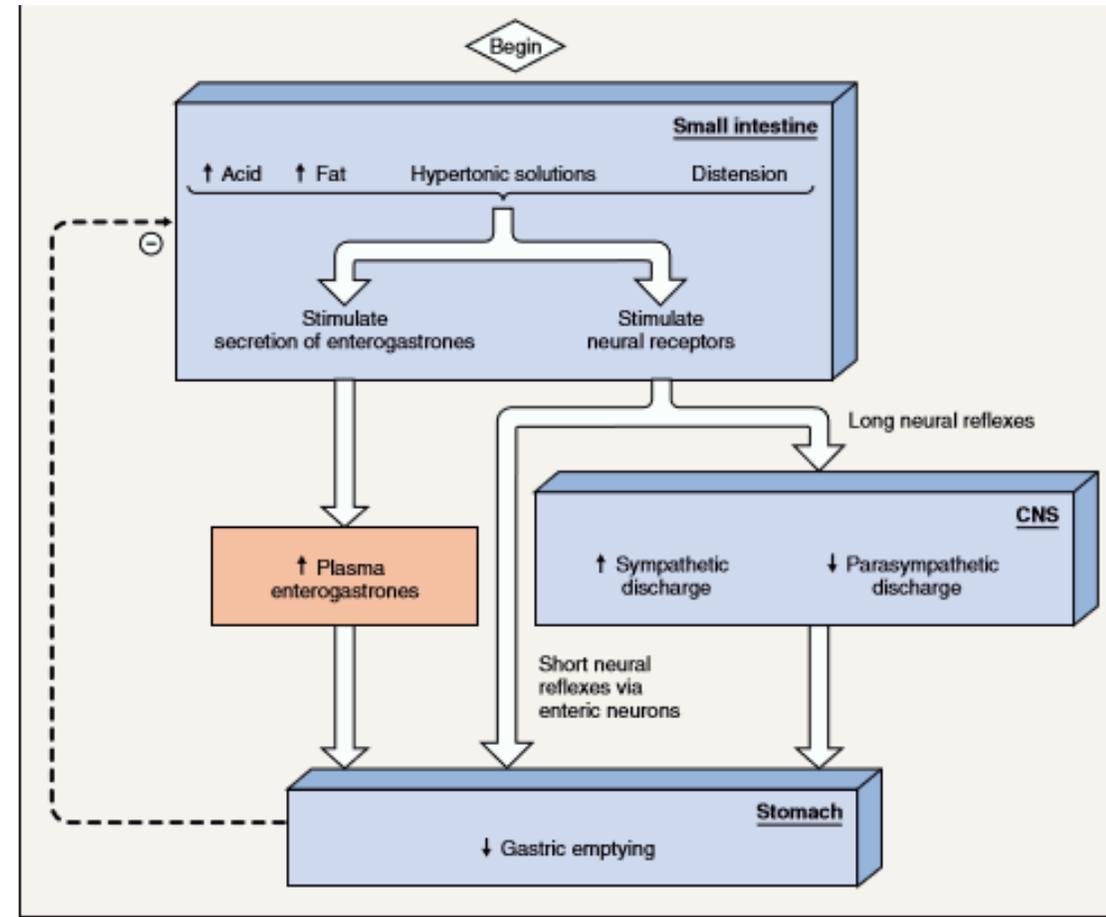
❖ What is responsible for producing gastric peristaltic waves?

- Their rhythm (three per minute) is generated by pacemaker cells in the longitudinal smooth muscle layer.
- These smooth-muscle cells undergo spontaneous depolarization-repolarization cycles (slow waves) known as the basic electrical rhythm of the stomach.
- These slow waves are conducted through gap junctions along the stomach's longitudinal muscle layer and also induce similar slow waves in the overlying circular muscle layer.



Gastric Motility

- **Gastrin** increases the force of antral smooth-muscle contractions.
- **Distension of the stomach** also increases the force of antral contractions through long and short reflexes triggered by mechanoreceptors in the stomach wall.
- In contrast, **distension of the duodenum or the presence of fat, high acidity, or hypertonic solutions in its lumen all inhibit gastric emptying.**
- **Decreased parasympathetic or increased sympathetic activity inhibits motility.**
- Via these pathways, pain and emotions such as sadness, depression, and fear tend to decrease motility, whereas aggression and anger tend to increase it.



Pancreatic Secretions

- The exocrine portion of the pancreas secretes **bicarbonate ions** and a **number of digestive enzymes** into ducts that converge into the pancreatic duct, the latter joining the common bile duct from the liver just before this duct enters the duodenum.
- **The enzymes are secreted by gland cells at the pancreatic end of the duct system, whereas bicarbonate ions are secreted by the epithelial cells lining the ducts.**
- **The mechanism of bicarbonate secretion is analogous to that of hydrochloric acid secretion by the stomach, except that the directions of hydrogen-ion and bicarbonate-ion movement are reversed.**
- The enzymes secreted by the pancreas digest fat, polysaccharides, proteins, and nucleic acids to fatty acids, sugars, amino acids, and nucleotides, respectively.
- The proteolytic enzymes are secreted in inactive forms (zymogens), as described for pepsinogen in the stomach, and then activated in the duodenum by other enzymes.
- **A key step in this activation is mediated by enterokinase**, which is embedded in the luminal plasma membranes of the intestinal epithelial cells.
- It is a proteolytic enzyme that splits off a peptide from pancreatic trypsinogen, forming the active enzyme trypsin.
- **Trypsin is also a proteolytic enzyme, and once activated, it activates the other pancreatic zymogens by splitting off peptide fragments.**

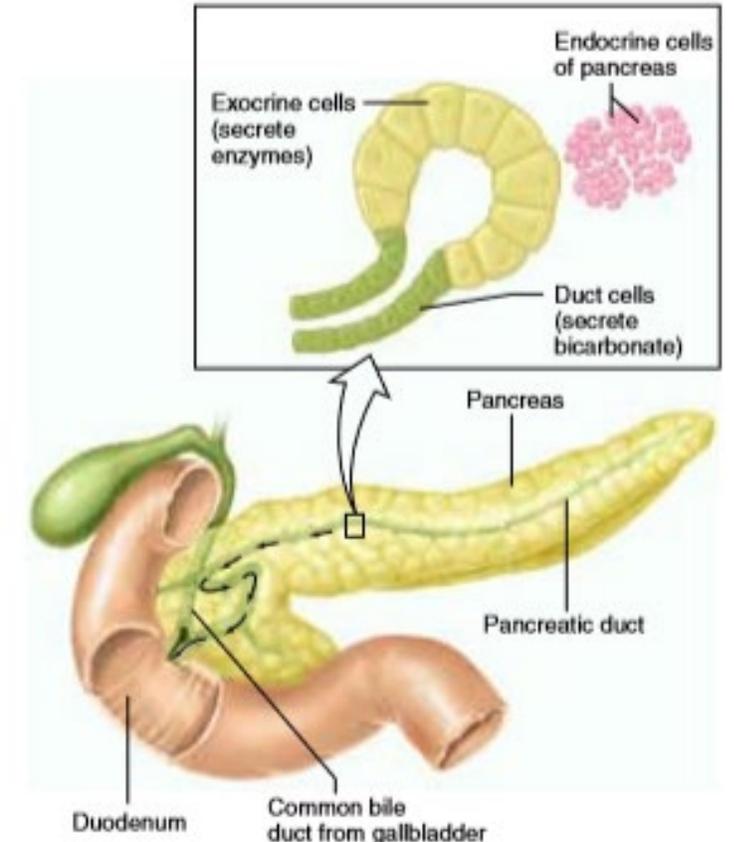
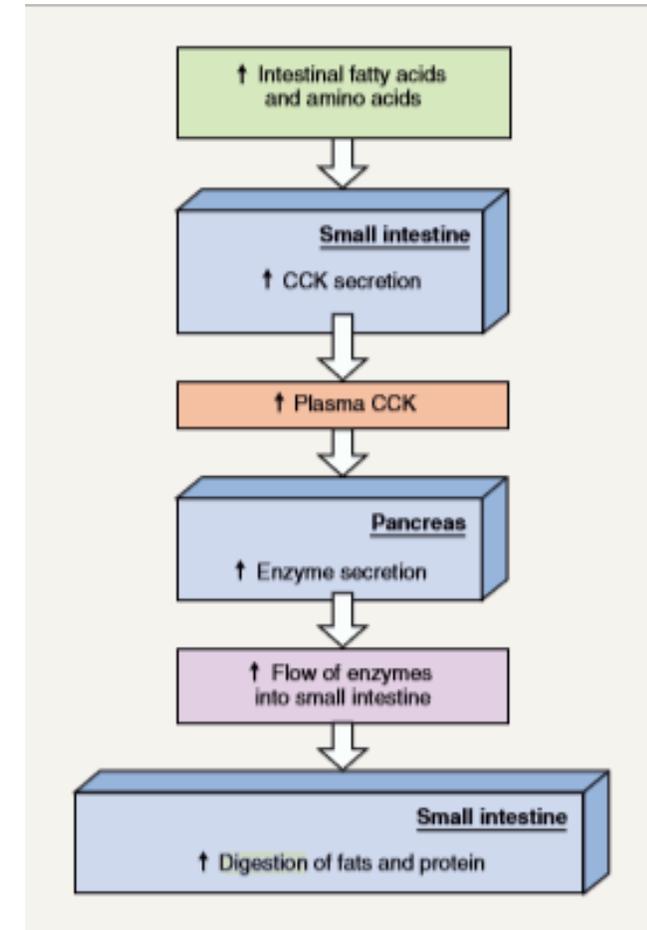


FIGURE 17-25
Structure of the pancreas. ⚡

Pancreatic Secretions

- **Pancreatic secretion increases during a meal, mainly as a result of stimulation by the hormones secretin and CCK.**
- **Secretin is the primary stimulant for bicarbonate secretion, whereas CCK mainly stimulates enzyme secretion.**
- **Since the function of pancreatic bicarbonate is to neutralize acid entering the duodenum from the stomach, the major stimulus for secretin release is increased acidity in the duodenum**
- **Since CCK stimulates the secretion of digestive enzymes, including those for fat and protein digestion, the stimuli for its release are fatty acids and amino acids in the duodenum.**
- Luminal acid and fatty acids also act on afferent nerve endings in the intestinal wall, initiating reflexes that act on the pancreas to increase both enzyme and bicarbonate secretion.
- Although most of the pancreatic exocrine secretions are controlled by stimuli arising from the intestinal phase of digestion, cephalic and gastric stimuli, by way of the parasympathetic nerves to the pancreas, also play a role. Thus, the taste of food or the distension of the stomach by food, will lead to increased pancreatic secretion.



Bile Secretion

- As stated earlier, bile is secreted by liver cells into a number of small ducts, the bile canaliculi which converge to form the common hepatic duct.
- **Bile contains six major ingredients:**
 - (1) bile salts;
 - (2) lecithin (a phospholipid);
 - (3) bicarbonate ions and other salts;
 - (4) cholesterol;
 - (5) bile pigments and small amounts of other metabolic end products, and
 - (6) trace metals.
- ❖ *From the standpoint of gastrointestinal function, the most important components of bile are the bile salts. During the digestion of a fatty meal, most of the bile salts entering the intestinal tract.*
- ❖ The absorbed bile salts are returned via the portal vein to the liver, where they are once again secreted into the bile.
- ❖ This recycling pathway from the intestine to the liver and back to the intestine is known as the **enterohepatic circulation**.
- ❖ A small amount (5 percent) of the bile salts escape this recycling and is lost in the feces, but the liver synthesizes new bile salts from cholesterol to replace them.
- ❖ During the digestion of a meal the entire bile salt content of the body may be recycled several times via the enterohepatic circulation.

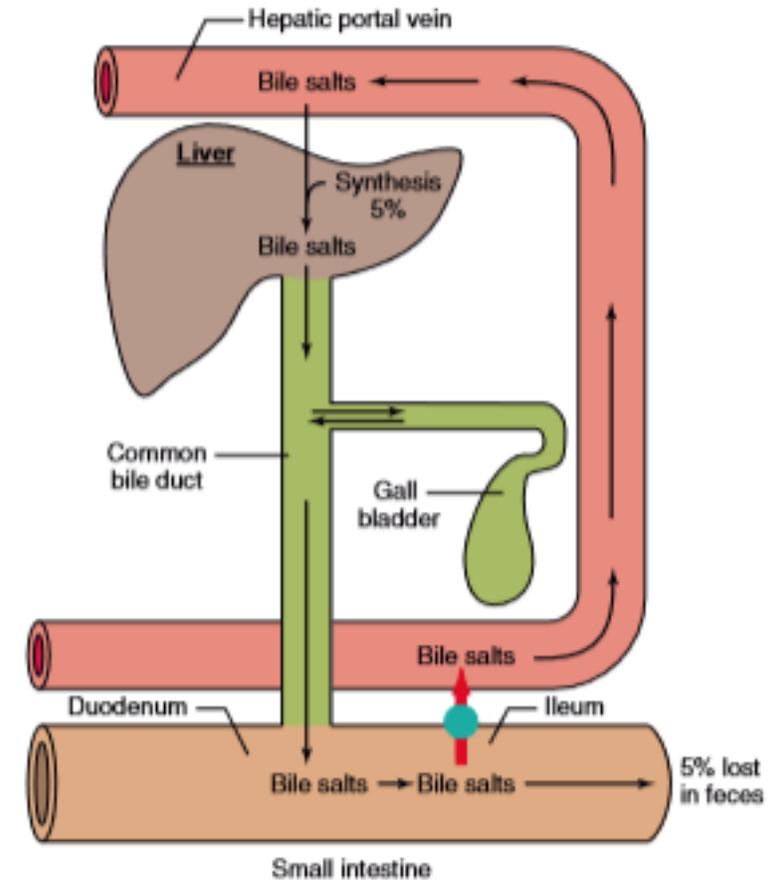
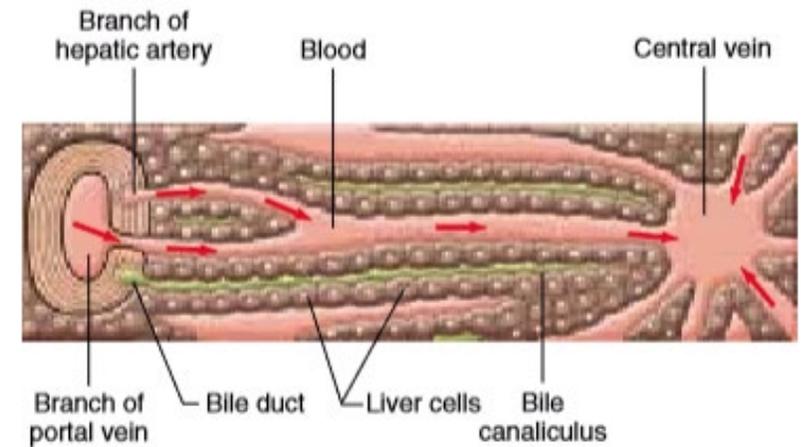


FIGURE 17-30
Enterohepatic circulation of bile salts.

Bile Secretion

- **Bile pigments are substances formed from the heme portion of hemoglobin** when old or damaged erythrocytes are digested in the spleen and liver.
- **The predominant bile pigment is bilirubin**, which is extracted from the blood by liver cells and actively secreted into the bile.
- **It is bilirubin that gives bile its yellow color.**
- **After entering the intestinal tract, bilirubin is modified by bacterial enzymes to form the Brown pigments that give feces their characteristic color.**
- **During their passage through the intestinal tract, some of the bile pigments are absorbed into the blood and are eventually excreted in the urine, giving urine its yellow color.**
- Like pancreatic secretions, the components of bile are secreted by two different cell types.
- The bile salts, cholesterol, lecithin, and bile pigments are secreted by hepatocytes (liver cells), whereas most of the bicarbonate-rich salt solution is secreted by the epithelial cells lining the bile ducts.
- Secretion of the salt solution by the bile ducts, just like that secreted by the pancreas, is stimulated by secretin in response to the presence of acid in the duodenum.



Bile Secretion

- Unlike the pancreas, whose secretions are controlled by intestinal hormones, bile salt secretion is controlled by the concentration of bile salts in the blood
- Absorption of bile salts from the intestine during the digestion of a meal leads to their increased plasma concentration and thus to an increased rate of bile salt secretion by the liver.
- Although bile secretion is greatest during and just after a meal, some bile is always being secreted by the liver.
- Surrounding the common bile duct at the point where it enters the duodenum is a ring of smooth muscle known as the sphincter of Oddi.
- When this sphincter is closed, the dilute bile secreted by the liver is shunted into the gallbladder where the organic components of bile become concentrated as NaCl and water are absorbed into the blood.
- Shortly after the beginning of a fatty meal, the sphincter of Oddi relaxes and the gallbladder contracts, discharging concentrated bile into the duodenum.
- The signal for gallbladder contraction and sphincter relaxation is the intestinal hormone CCK— (It is from this ability to cause contraction of the gallbladder that cholecystokinin received its name: chole, bile; cysto,

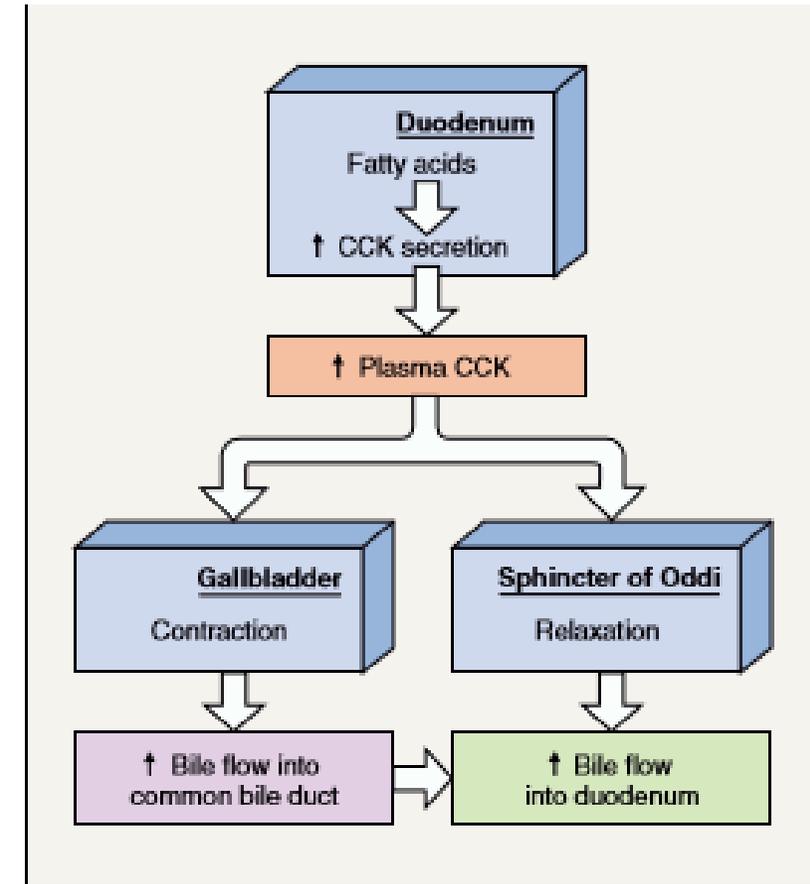
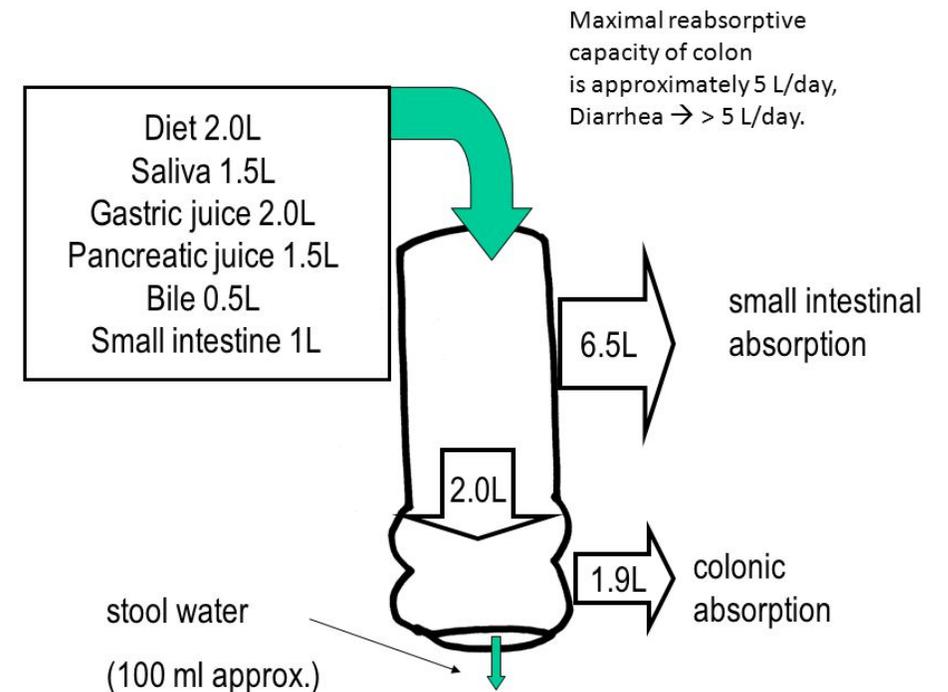


FIGURE 17-31

Small Intestine Secretion

- Approximately 1500 ml of fluid is secreted by the walls of the small intestine from the blood into the lumen each day.
- One of the reasons for water movement into the lumen (secretion) is that the intestinal epithelium at the base of the villi secretes a number of mineral ions, notably sodium, chloride, and bicarbonate ions into the lumen, and water follows by osmosis.
- These secretions, along with mucus, lubricate the surface of the intestinal tract and help protect the epithelial cells from excessive damage by the digestive enzymes in the lumen.
- Various hormonal and paracrine signals—as well as certain bacterial toxins—can increase the opening frequency of these channels and thus increase fluid secretion.
- Water movement into the lumen also occurs when the chyme entering the small intestine from the stomach is hypertonic because of a high concentration of solutes in the meal and because digestion breaks down large molecules into many more small molecule.
- This hypertonicity causes the osmotic movement of water from the isotonic plasma into the intestinal lumen.

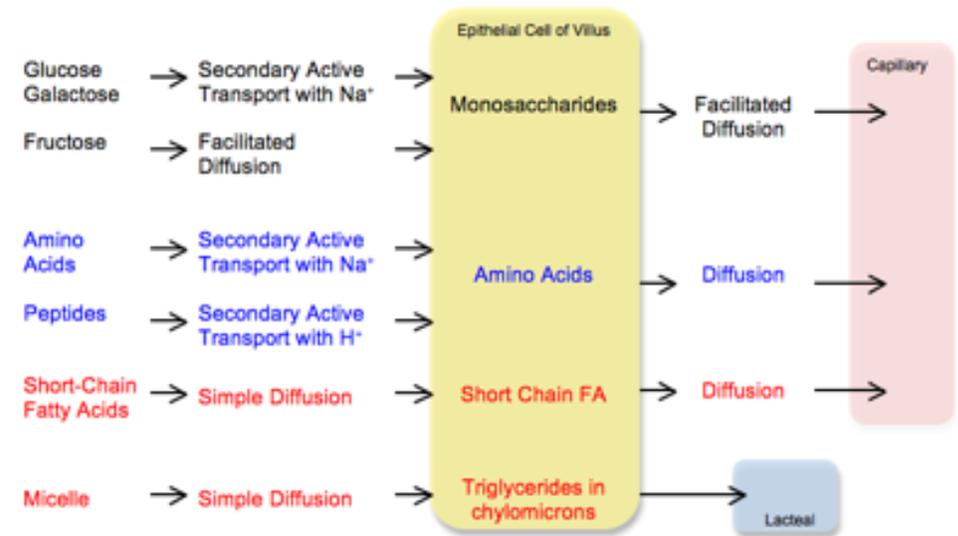
Overview Of Intestinal Fluid Transport



Small Intestine Absorption

- Normally, virtually all of the fluid secreted by the small intestine is absorbed back into the blood.
- In addition, a much larger volume of fluid, which includes salivary, gastric, hepatic, and pancreatic secretions, as well as ingested water, is simultaneously absorbed from the intestinal lumen into the blood.
- Thus, overall there is a large net absorption of water from the small intestine.
- Absorption is achieved by the transport of ions, primarily sodium, from the intestinal lumen into the blood, with water following by osmosis.

Absorption in the Small Intestine



Motility

- The most common motion in the small intestine during digestion of a meal is a stationary contraction and relaxation of intestinal segments, with little apparent net movement toward the large intestine.
- Each contracting segment is only a few centimeters long, and the contraction lasts a few seconds.
- The chyme in the lumen of a contracting segment is forced both up and down the intestine.
- This rhythmical contraction and relaxation of the intestine, known as segmentation, produces a continuous division and subdivision of the intestinal contents, thoroughly mixing the chyme in the lumen and bringing it into contact with the intestinal wall.
- These segmenting movements are initiated by electrical activity generated by pacemaker cells in or associated with the circular smooth-muscle layer.
- The intestinal rhythm varies along the length of the intestine, each successive region having a slightly lower frequency than the one above.
- For example, segmentation in the duodenum occurs at a frequency of about 12 contractions/min, whereas in the last portion of the ileum the rate is only 9 contractions/min.

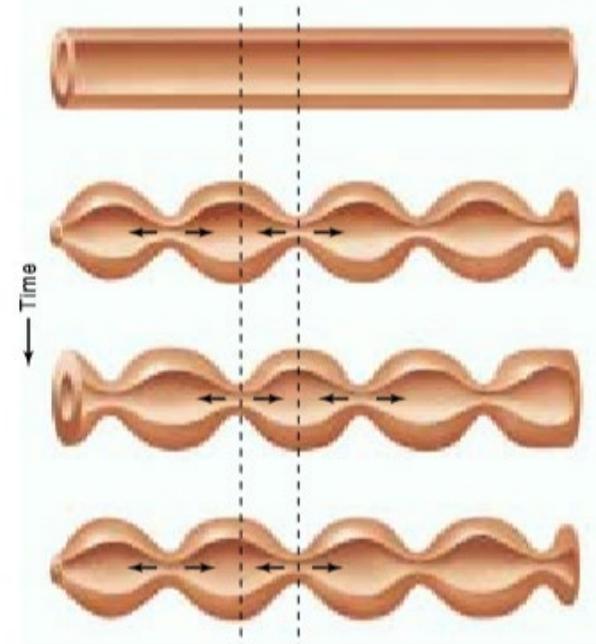
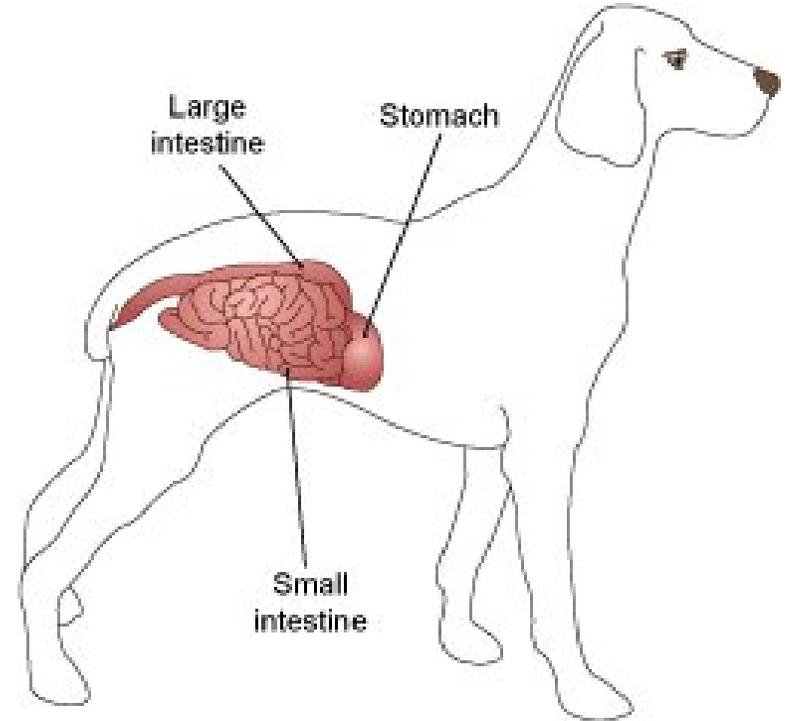


FIGURE 17-32

Segmentation movements of the small intestine in which segments of the intestine contract and relax in a rhythmical pattern but do not undergo peristalsis. This is the pattern encountered during a meal, which mixes the luminal contents. 

Large Intestine

- Although the large intestine has a greater diameter than the small intestine, its epithelial surface area is far less, since *the large intestine is about half as long as the small intestine, its surface is not convoluted, and its mucosa lacks villi.*
- The secretions of the large intestine are scanty, lack digestive enzymes, and consist mostly of mucus and fluid containing bicarbonate and potassium ions.
- The primary function of the large intestine is to store and concentrate fecal material before defecation.

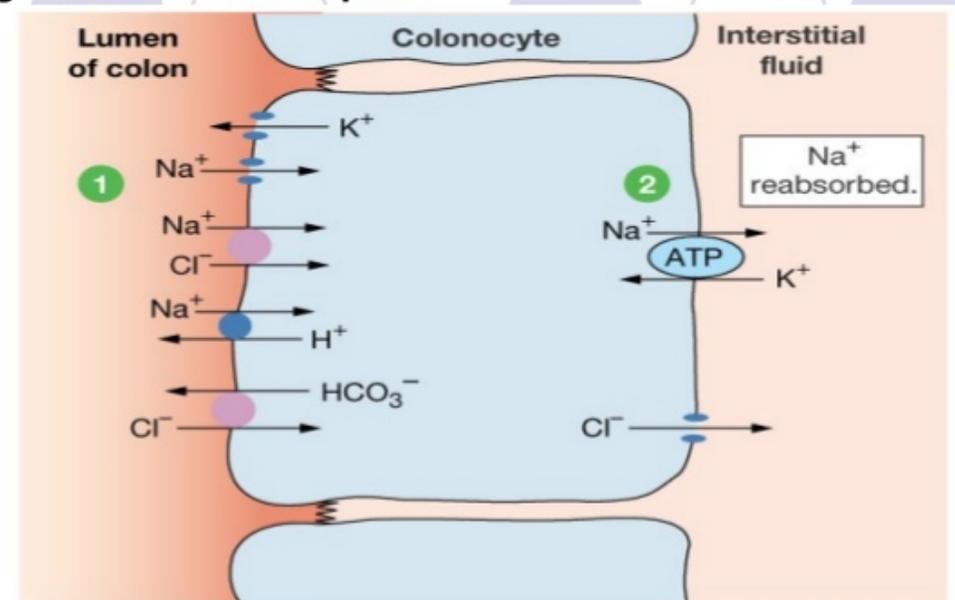


Used Under License
Copyright© Lifelearn Inc.

Large Intestine

- Chyme enters the cecum through the ileocecal sphincter.
- This sphincter is normally closed, but after a meal, when the gastroileal reflex increases ileal contractions.
- **Distension of the large intestine produces a reflex contraction of the sphincter, preventing fecal material from moving back into the small intestine.**
- Fluid absorption by the large intestine normally accounts for only a small fraction of the fluid entering the gastrointestinal tract each day.
- The primary absorptive process in the large intestine is the active transport of sodium from lumen to blood, with the accompanying osmotic absorption of water.
- If fecal material remains in the large intestine for a long time, almost all the water is absorbed, leaving behind hard fecal pellets.

Large Intestine Absorption

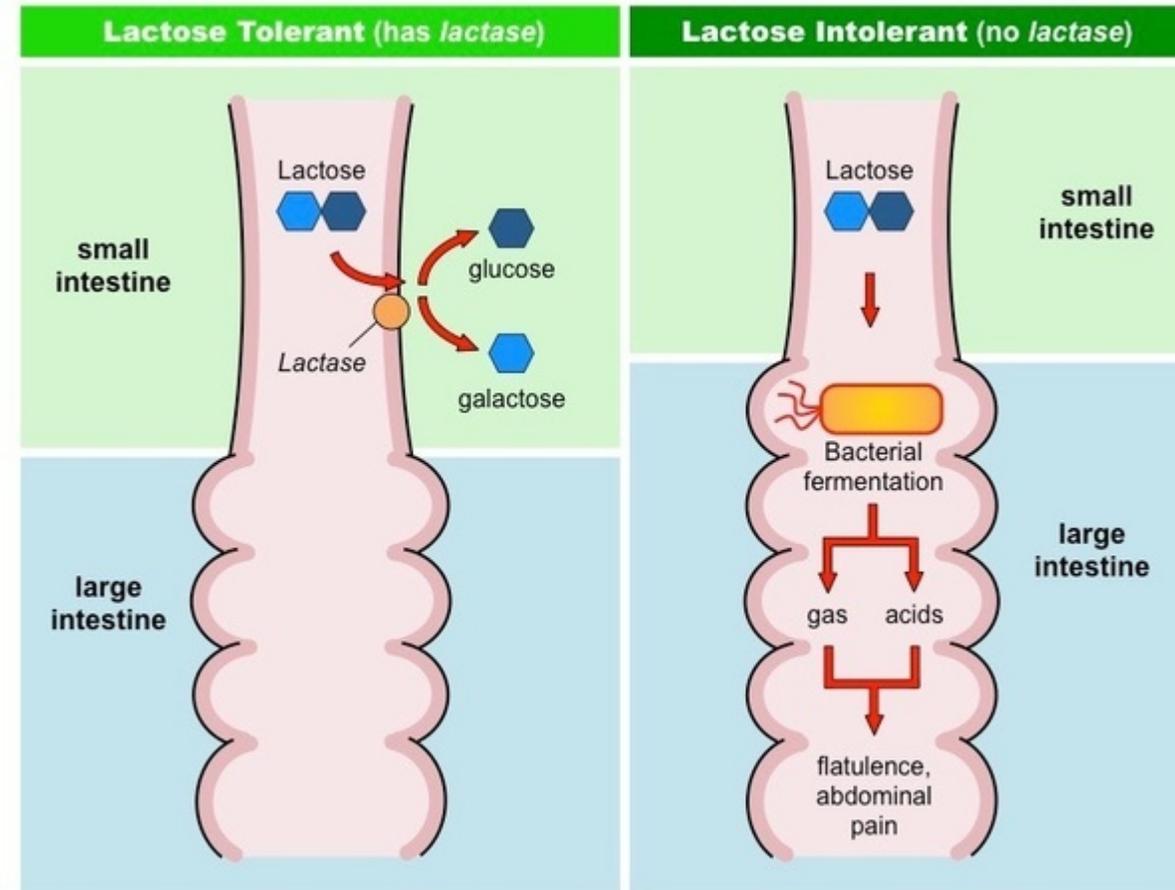


1 Na⁺ enters colonic cells by multiple pathways.

2 The Na⁺-K⁺-ATPase pumps Na⁺ into the ECF.

Large Intestine

- The large intestine also absorbs some of the products formed by the bacteria inhabiting this region.
- **Undigested polysaccharides (fiber) are metabolized to short-chain fatty acids by bacteria in the large intestine and absorbed by passive diffusion.**
- The bicarbonate secreted by the large intestine helps to neutralize the increased acidity resulting from the formation of these fatty acids.
- These bacteria also produce small amounts of vitamins, especially vitamin K, that can be absorbed into the blood.
- Other bacterial products include gas (flatus), which is a mixture of nitrogen and carbon dioxide, with small amounts of the inflammable gases hydrogen, methane, and hydrogen sulfide.



Horse Cecum And Colon

- The horse is a hindgut fermenter with a cecum and ascending colon specially adapted to allow fermentation of plant cellulose and hemicellulose, providing the horse with energy in the form of volatile fatty acids.
- **The hindgut strategy for obtaining energy from plant structural carbohydrates is also found in the rabbit, chinchilla, koala, elephant, and rhinoceros.**
- **The cecum fills by gravity in the horse.**
- Segmental contractions assure mixing of ingesta with bacteria to promote fermentation, and peristaltic contractions beginning near the apex can move material up and out of the cecum to the right side of the ventral colon.
- The orifice joining the cecum and colon is the cecocolic orifice and is a relatively small opening.
- This point of resistance to the flow of material can result in obstruction of cecal emptying and the ensuing cecal distension is a common cause of colic in horses.

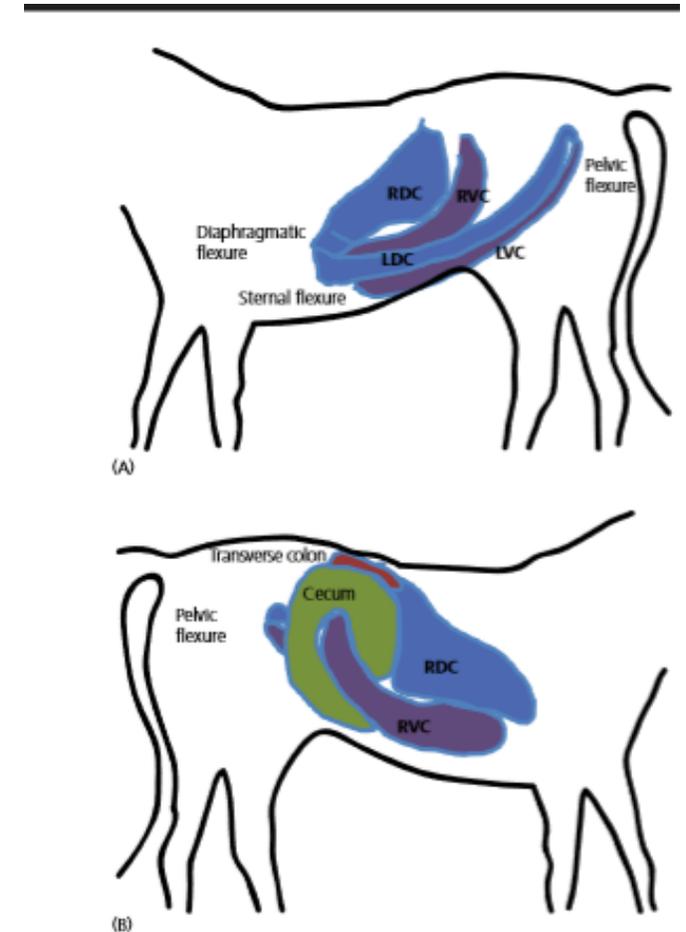
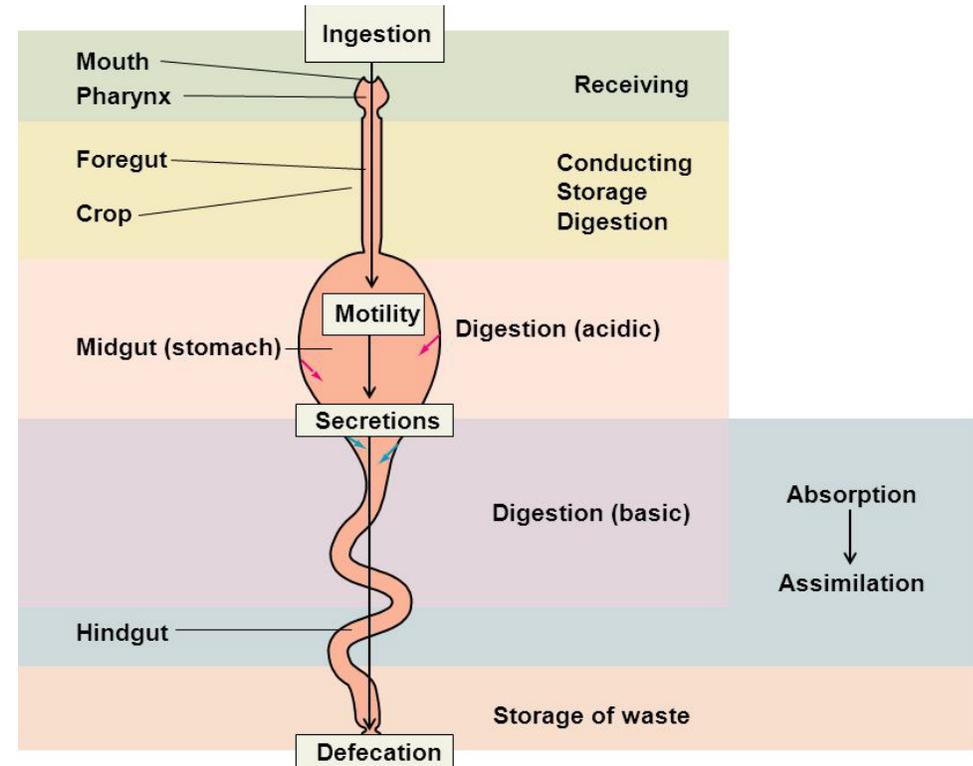


Figure 42.11 Horse hindgut. (A) Left-sided view of ventral and dorsal colons of horse. Cecal matter enters the right ventral colon. Cecum removed for clarity. (B) Right-sided view of cecum, right ventral and right dorsal colon leading into the transverse colon. LDC, left dorsal colon; LVC, left ventral colon; RDC, right dorsal colon; RVC, right ventral colon.

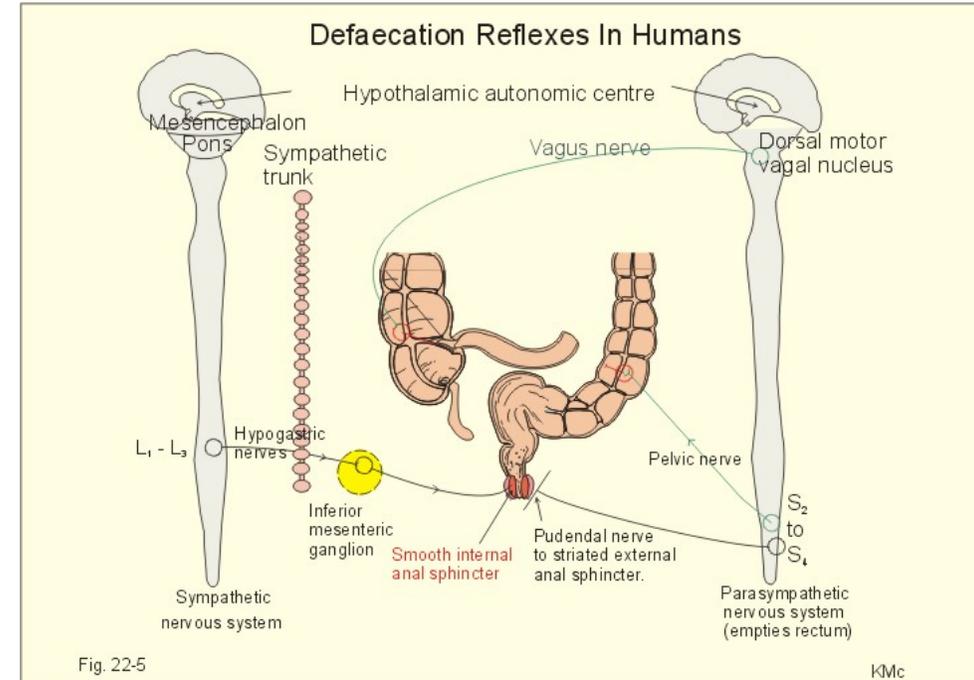
Motility and Defecation

- Contractions of the circular smooth muscle in the large intestine produce a segmentation motion with a rhythm considerably slower (one every 30 min) than that in the small intestine.
- Because of the slow propulsion of the large intestine contents, material entering the large intestine from the small intestine remains for about 18 to 24 h - This provides time for bacteria to grow and multiply.
- Three to four times a day, generally following a meal, a wave of intense contraction, known as a mass movement, spreads rapidly over the transverse segment of the large intestine toward the rectum.
- Unlike a peristaltic wave, in which the smooth muscle at each point relaxes after the wave of contraction has passed, the smooth muscle of the large intestine remains contracted for some time after a mass movement.



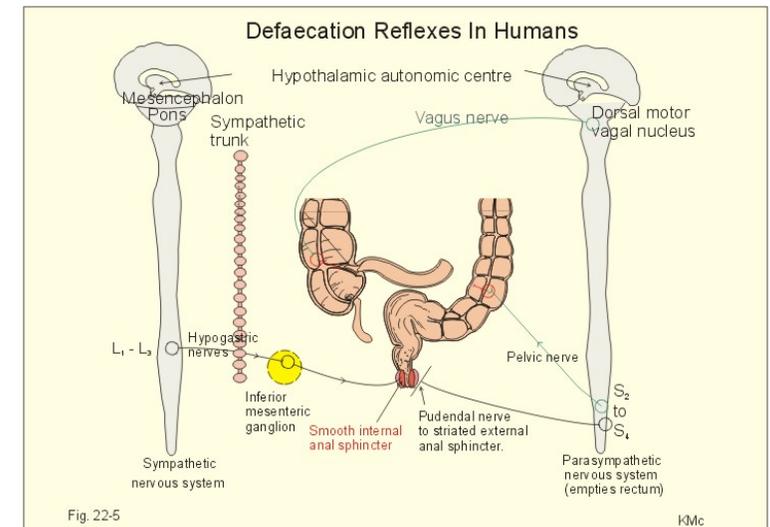
Motility and Defecation

- The anus, the exit from the rectum, is normally closed by the internal anal sphincter, which is composed of smooth muscle, and the external anal sphincter, which is composed of skeletal muscle under voluntary control.
- The sudden distension of the walls of the rectum produced by the mass movement of fecal material into it initiates the neurally mediated defecation reflex.
- The conscious urge to defecate, mediated by mechanoreceptors, accompanies distension of the rectum.
- The reflex response consists of a contraction of the rectum, relaxation of the internal anal sphincter, but contraction of the external anal sphincter (initially), and increased peristaltic activity in the sigmoid colon.
- Eventually, a pressure is reached in the rectum that triggers reflex relaxation of the external anal sphincter, allowing the feces to be expelled.



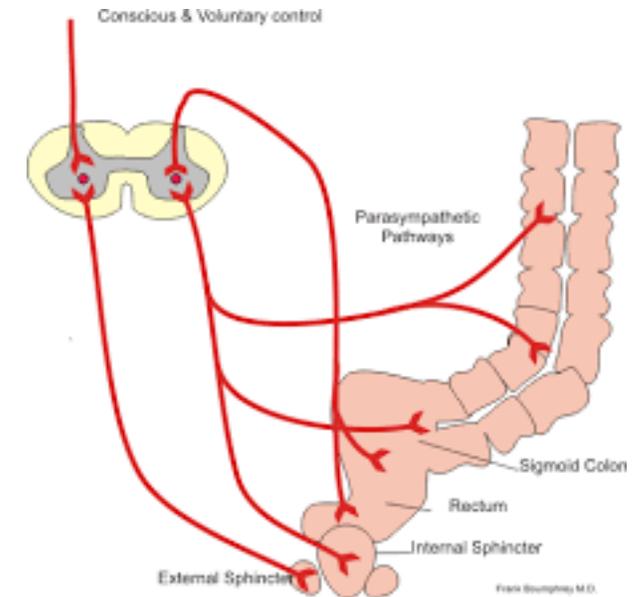
Motility and Defecation

- Brain centers can, however, via descending pathways to somatic nerves to the external anal sphincter, override the reflex signals that eventually would relax the sphincter, thereby keeping the external sphincter closed and allowing a person to delay defecation.
- In this case, the prolonged distension of the rectum initiates a reverse peristalsis, driving the rectal contents back into the sigmoid colon.
- The urge to defecate then subsides until the next mass movement again propels more feces into the rectum, increasing its volume and again initiating the defecation reflex.



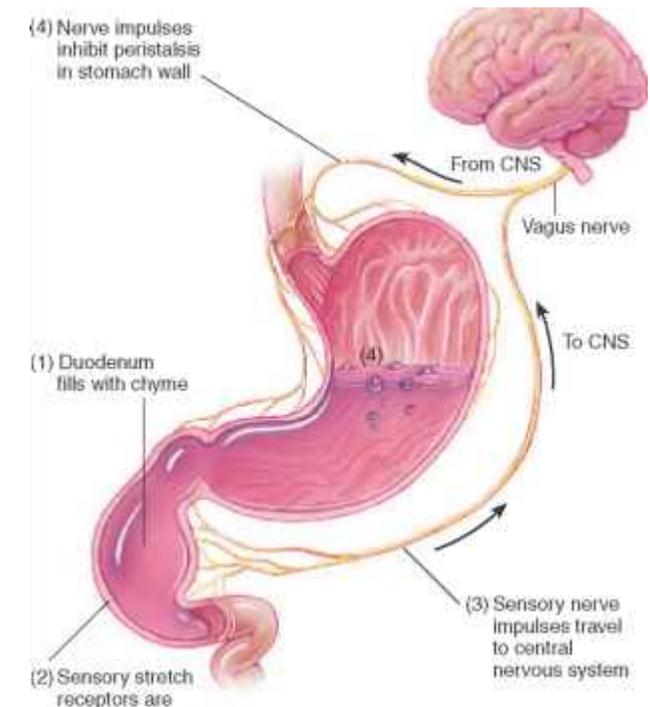
Motility and Defecation

- Defecation is normally assisted by a deep inspiration, followed by closure of the glottis and contraction of the abdominal and thoracic muscles, producing an increase in abdominal pressure that is transmitted to the contents of the large intestine and rectum.
- This maneuver (termed the Valsalva maneuver) also causes a rise in intrathoracic pressure, which leads to a transient rise in blood pressure followed by a fall in pressure as the venous return to the heart is decreased.
- The cardiovascular changes resulting from excessive strain during defecation may precipitate a stroke or heart attack, especially in constipated elderly individuals with cardiovascular disease.



Vomition

- Carnivores and most omnivore mammals have the ability to vomit (also called emesis).
- Some species may use the stomach as a means of conveyance of food to their offspring. They may vomit the contents of the stomach on stimulation by the sight and sound of their offspring. This is generally referred to as regurgitation rather than vomition or emesis.
- In most species vomition serves primarily as a means of removing toxic material from the stomach.
- Vomition is a rather complex reflex controlled by collections of neurons (nuclei) residing in the medulla.
- These neurons receive sensory information directly from the gastrointestinal tract via vagal and sympathetic afferent fibers.
- Stomach and oropharynx irritants, such as hydrogen peroxide, syrup of Ipecac, and salt, can activate the vomiting reflex within the vomiting center.
- A second collection of nerves within the floor of the fourth ventricle forms the chemoreceptor trigger zone. These neurons have receptors that recognize blood-borne chemicals or toxins that reach them. One chemical recognized by the chemoreceptor trigger zone and used by veterinarians to induce vomiting is the opiate apomorphine,
- Xylazine, an α_2 -receptor agonist, is also a reliable emetic agent, particularly in cats.
- The chemoreceptor trigger zone can also receive input from higher centers of the brain so that certain smells or sights can initiate vomition.
- The vestibular apparatus also sends signals to the chemoreceptor trigger zone, and motion sickness or disturbances within the middle ear, such as infection, can cause vomition.



Vomition

- The vomiting reflex begins when the vomiting center neurons have been stimulated.
- The muscles in the pyloric end of the stomach and sometimes even the upper duodenum contract, sending ingesta toward the esophageal end of the stomach.
- The rest of the stomach and the lower esophageal sphincter relax allowing some stomach contents into the esophagus.
- However, at least initially, the esophagus responds by initiating peristaltic contractions to push the stomach contents back into the stomach.
- **This process is called retching and will occur several times before true vomition occurs.**
- During one of the next contractions that arise from the pyloric stomach the reflex will also induce strong contractions of the diaphragm and abdominal muscles that raise the pressure inside the stomach and esophagus and overcome esophageal peristalsis to propel the stomach contents out of the mouth.
- At the same moment, the upper esophageal sphincter relaxes, the nasopharynx closes to prevent material exiting via the nasal cavities, and the glottis closes to prevent entry of material into the trachea.



©Warren Photographie

Vomition

- Some species of animals are unable to vomit.
- **Rats** are unable to vomit because they do not have nuclei within their medulla that form the vomiting center. They are therefore unable to coordinate diaphragm and abdominal muscle contraction with contraction of the stomach.
- They also cannot coordinate contraction of the stomach and opening of lower and upper esophageal sphincters.
- **Rabbits** cannot vomit either.
- They do have a vomiting center in the medulla but have a lower esophageal sphincter that they cannot relax enough to allow vomition.
- **Horses** also cannot vomit, despite having a vomiting center. Some researchers suggest that they also have a lower esophageal sphincter that will not relax.
- Other researchers have suggested that the angle of entry of the esophagus into the stomach becomes even more acute (kinked) when the stomach is full, preventing the horse from vomiting an excessive meal of grain for example.
- The horse stomach does not distend very much and the full stomach can distend to the point of initiating a vomition reflex.
- The stomach will try to contract (causing colic pain) and the abdominal muscles will contract but stomach contents cannot pass the lower esophageal sphincter.
- The horse's abdominal muscles are so strong that prolonged attempts to vomit can cause the stomach wall to rupture.

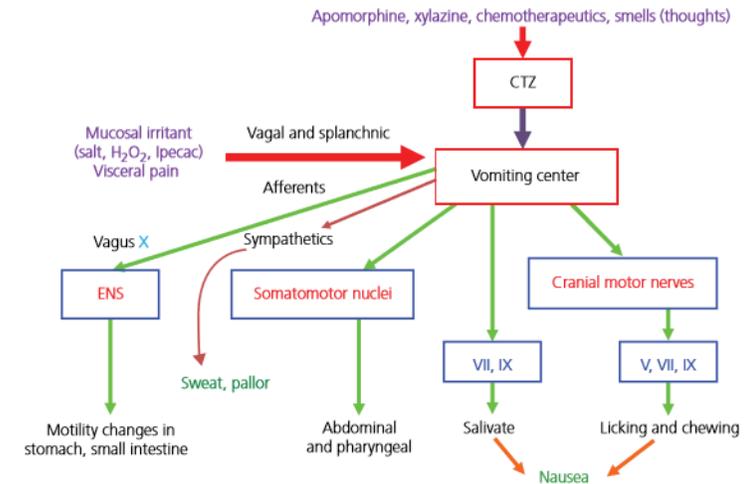
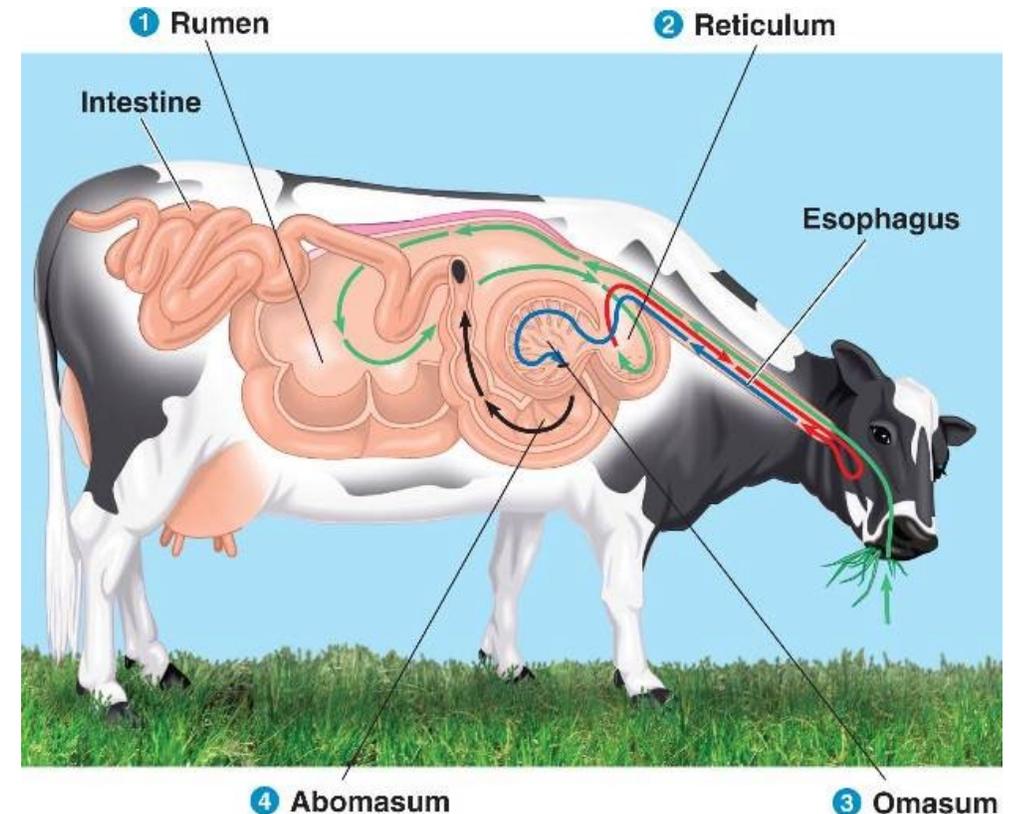


Figure 42.8 Vomition. Neurons within the chemoreceptor trigger zone (CTZ) respond to blood-borne chemicals and send input to a vomiting center in the medulla. The vomiting center also receives direct input from vagal and splanchnic afferents that indicate the presence of some irritant in the stomach. The vomiting center initiates widespread parasympathetic and sympathetic discharge resulting in sweating, nausea, and salivation. Finally the coordinated contraction of the stomach and abdominal muscles forces stomach contents up the esophagus and out of the mouth.

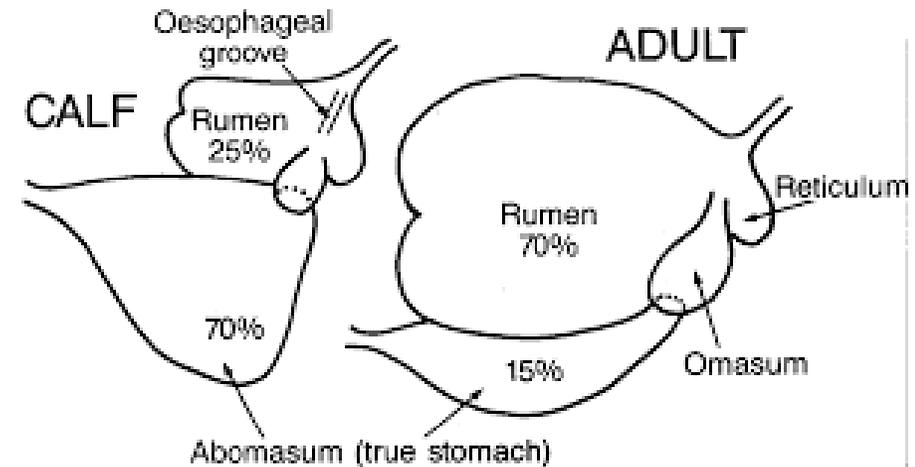
Ruminant Digestive Physiology and Intestinal Microbiology

- Ruminants are a widespread and diverse group of mammals.
- Domesticated species such as the cow, sheep, goat, water buffalo, and camel utilize plant structural carbohydrates to provide the energy to produce milk and meat for human consumption.
- Ruminants all have a common feature: *they have specially adapted outcroppings of the esophagus called **forestomachs** that allow storage of ingesta and permit bacterial fermentation to digest materials that mammalian enzymes cannot break down.*
- There are variations in the shape and size of the various esophageal structures utilized as fermentation vats by ruminants.
- The cow's anatomy will be used to illustrate basic principles shared by most of the ruminants.



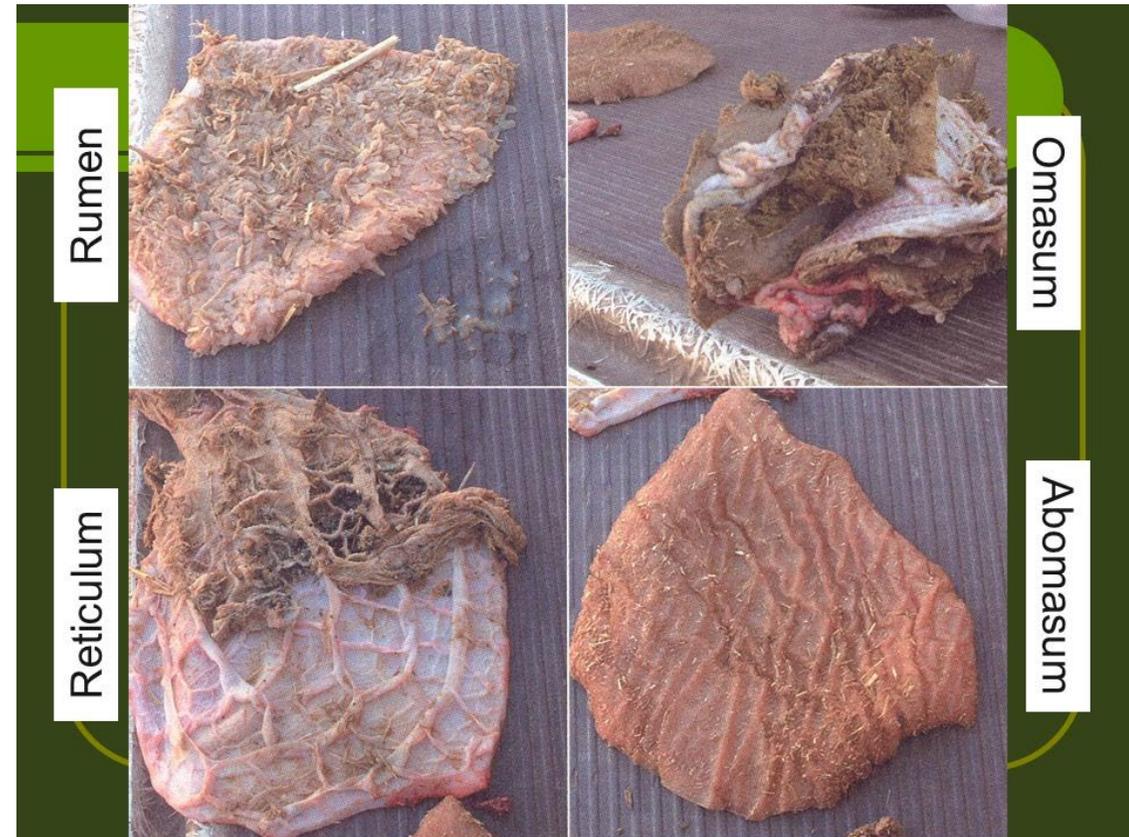
Forestomachs of the cow

- The rumen is the largest compartment and is lined with papillae
- Papillae extend from the rumen wall to increase the surface area for absorption.
- Rumen papillae are practically absent from the neonatal rumen.
- The length and width of rumen papillae increases as the rumen becomes populated with bacteria and as the neonate is placed on a diet that promotes production of **butyrate** in the rumen.
- Butyrate is a volatile fatty acid (VFA) that is vital to the integrity of the epithelium of the rumen.



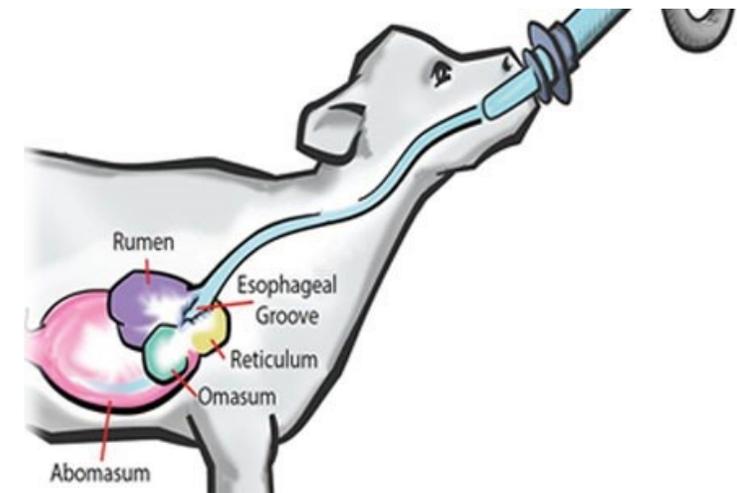
Forestomachs of the cow

- The most cranial section of the large fermentation vat is called the **reticulum**.
- It is distinguishable from the rumen by the unique **honeycomb-shaped** projections from its wall.
- **Functionally, the rumen and reticulum are the same: both serve as sites of storage of ingesta and provide a safe haven for the bacteria unique to the rumen that will ferment the plant cellulose and hemicellulose of their diet.**
- They are both lined by stratified squamous epithelium that is capable of absorbing VFAs and some electrolytes and minerals.
- After fermentation in the rumen–reticulum, the more liquid portion of the fermentation mixture moves to the third forestomach, **the omasum**, through the reticulo-omasal orifice.
- The omasum is built very much like an automobile oil filter.
- It has long leaves covered by a stratified squamous epithelium that the juices leaving the rumen and reticulum must pass over on their way to the true stomach, known as the abomasum in ruminants .
- The leaves of the omasum can also absorb VFAs and water.



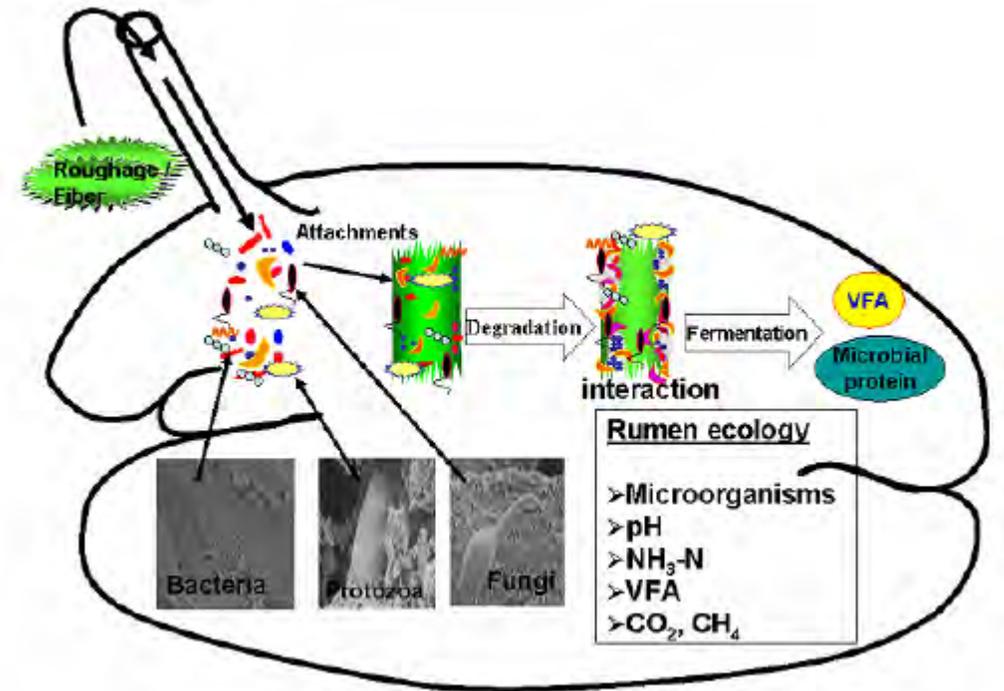
Forestomachs of the cow

- The abomasum is a true, glandular stomach which secretes acid and otherwise functions very similarly to the stomach of a monogastric.
- One fascinating specialization of this organ relates to its need to process large masses of bacteria. In contrast to the stomach of non-ruminants, [the abomasum secretes lysozyme](#), an enzyme that efficiently breaks down bacterial cell walls.
- The processes described above apply to adult ruminants.
- For the first month or so of life, the ruminant is functionally a monogastric.
- The forestomachs are formed, but are not yet fully developed. If milk is introduced into such a rumen, it basically rots rather than being fermented.
- To avoid this problem in such young ruminants, suckling causes a reflex closure of muscular folds that form a channel from the esophageal orifice toward the omasum (the esophageal groove), shunting milk away from the rumen and straight toward the stomach where it can be curdled by [rennin](#) and eventually digested enzymatically.



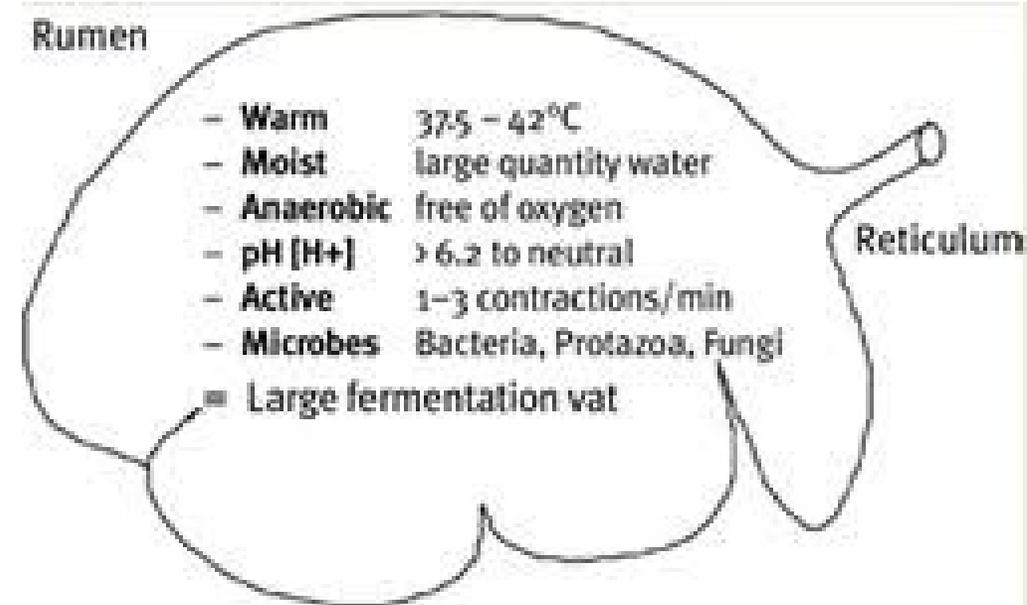
Rumen fermentation

- From the cow's perspective, a major advantage of having a rumen is to provide a home to the bacteria that possess the enzymes needed to break the $\beta(1\rightarrow4)$ linkages between the various sugars that make up cellulose (mostly hexoses such as glucose) and hemicellulose (mostly pentoses such as xylose and arabinose).
- Mammalian enzymes cannot perform this task.
- The cellulolytic bacteria that can break these bonds are very strict anaerobes and most are members of the Bacteroides, Ruminococcus and Butyrovibrio genera.
- They break the $\beta(1\rightarrow4)$ linkages of plant cell wall structural carbohydrates and utilize the liberated hexoses and pentoses to provide them with energy.
- However, because they are anaerobes living in an anaerobic environment, the end products of their fermentation are primarily the VFAs **acetate, propionate, and butyrate**.
- The VFAs are rapidly absorbed by nonionic diffusion across the forestomach epithelium and used by the ruminant for energy (discussed in more detail in the section on VFA absorption).
- **The rumen stays “healthy” so long as average pH stays above 5.7.**



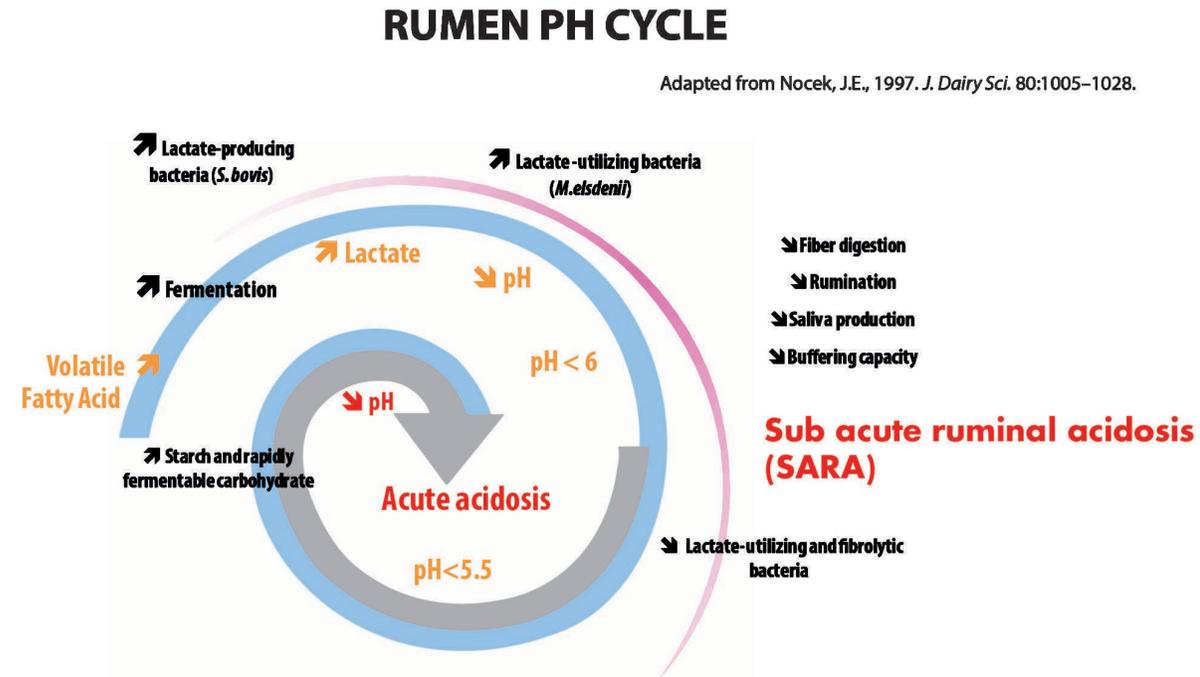
The rumen environment

- The rumen environment appears to be controlled by:
 - The type and quantity of food eaten
 - Periodic mixing through contraction of the rumen
 - Salivation and rumination
 - Diffusion or secretion into the rumen
 - Absorption of nutrients from the rumen
 - Passage of material down the digestive tract.
- Only under abnormal circumstances is this environment drastically perturbed.
- For instance, if grain is suddenly introduced into the diet, lacticacidaemia may occur because of a drop in ruminal pH, growth of *Streptococcus bovis* and the accumulation of lactic acid.



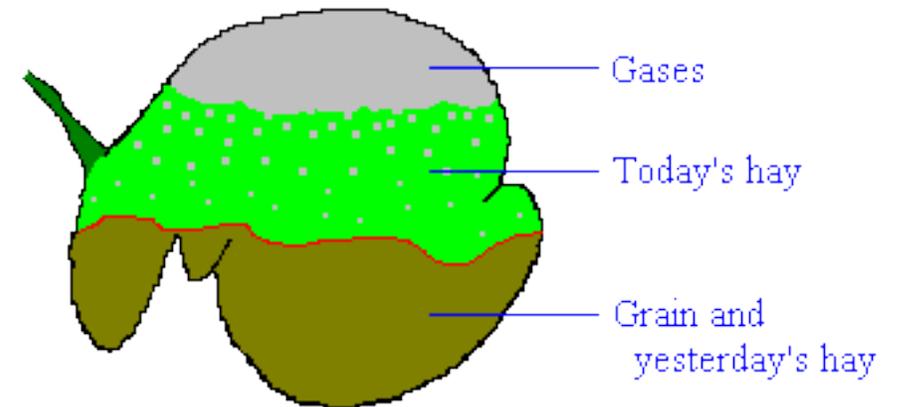
Lactate utilizers

- When the amount of grain in the diet is increased slowly over a period of weeks, it allows populations of bacteria known as lactate utilizers to populate the rumen.
- These bacteria metabolize the rumen fluid lactate as an energy source.
- The lactate utilizers belong to the *Selenomonas* and *Megasphaera* genera.
- Horses and other hindgut fermenters have essentially the same types of cellulolytic bacteria living in their cecum and colon as cows have in their rumen.
- However, in these species starches and sugars are absorbed by the small intestine before they reach the colon so the risk for very low pH is reduced.



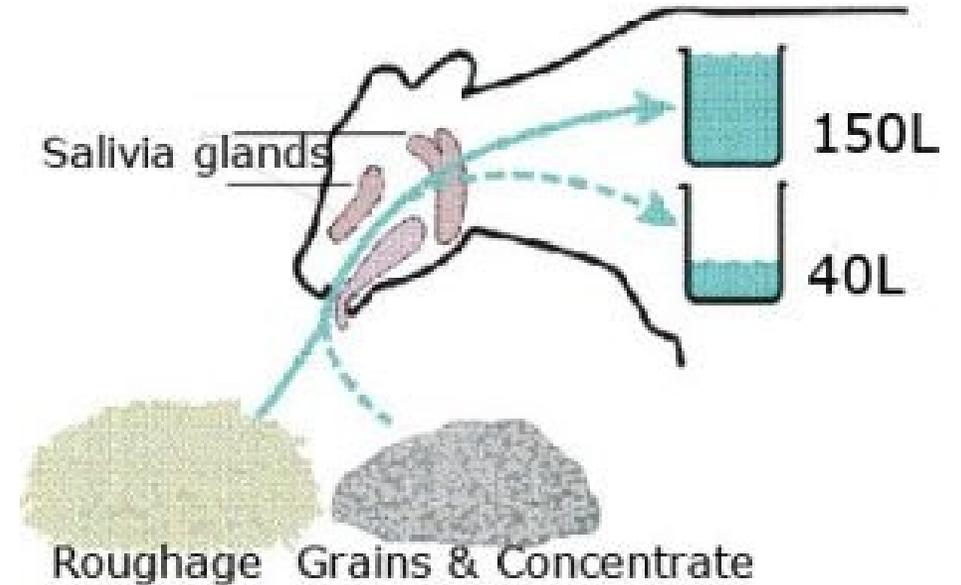
Dynamics of Cranial Digestion

- Feed, water and saliva are delivered to the reticulorumen through the esophageal orifice.
- Heavy objects (grain, rocks, nails) fall into the reticulum, while lighter material (grass, hay) enters the rumen proper.
- Added to this mixture are voluminous quantities of gas produced during fermentation.
- Ruminants produce prodigious quantities of saliva.
- Published estimates for adult cows are in the range of 100 to 150 liters of saliva per day!
- Aside from its normal lubricating qualities, saliva serves at least two very important functions in the ruminant:
 - provision of fluid for the fermentation vat
 - alkaline buffering - saliva is rich in bicarbonate, which buffers the large quantity of acid produced in the rumen and is probably critical for maintenance of rumen pH.
- All these materials within the rumen partition into three primary zones based on their specific gravity. Gas rises to fill the upper regions, grain and fluid-saturated roughage ("yesterday's hay") sink to the bottom, and newly arrived roughage floats in a middle layer.



Saliva in the rumen environment

- Saliva is continuously added to the rumen and maintains the contents in a fluid state, so facilitating access of micro-organisms to the plant materials.
- The volume of saliva secreted by ruminants is dependent on diet.
- The microbial community also affects salivary flow, which may be reduced by the presence of a population of protozoa.
- These rapidly assimilate starch and sugars and remove the need for copious salivation to maintain rumen pH.
- **The saliva is a buffered bicarbonate solution of about pH 8 containing high concentrations of sodium and phosphate ions.**



Reticuloruminal Motility

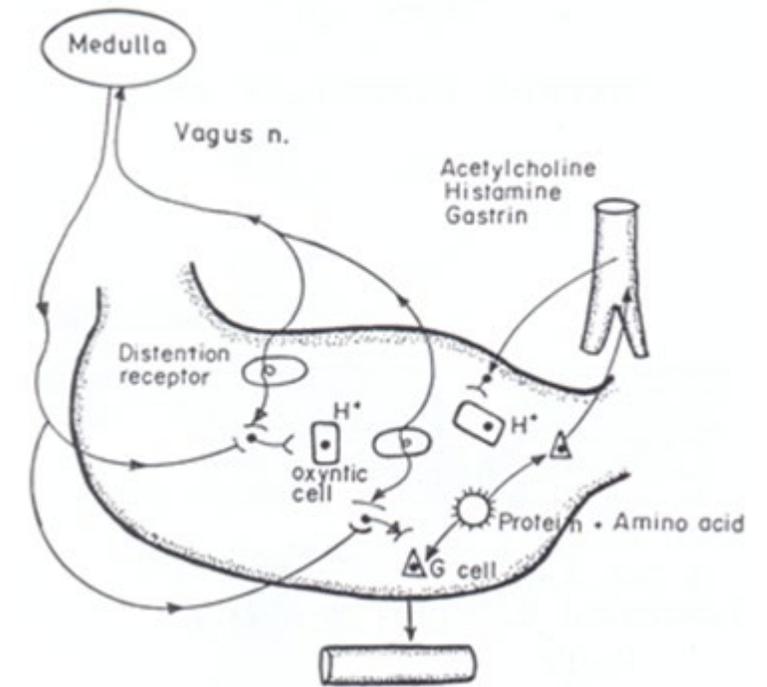
- An orderly pattern of ruminal motility is initiated early in life and, except for temporary periods of disruption, persists for the lifetime of the animal.
- These movements serve to mix the ingesta, aid in eructation of gas, and propel fluid and fermented foodstuffs into the omasum.
- If motility is suppressed for a significant length of time, ruminal impaction may result.
- A cycle of contractions occurs 1 to 3 times per minute. The highest frequency is seen during feeding, and the lowest when the animal is resting. Two types of contractions are identified:
- **Primary contractions** originate in the reticulum and pass caudally around the rumen. This process involves a wave of contraction followed by a wave of relaxation, so as parts of the rumen are contracting, other sacs are dilating.
- **Secondary contractions** occur in only parts of the rumen and are usually associated with eructation.



Contractions of the
ruminoreticulum

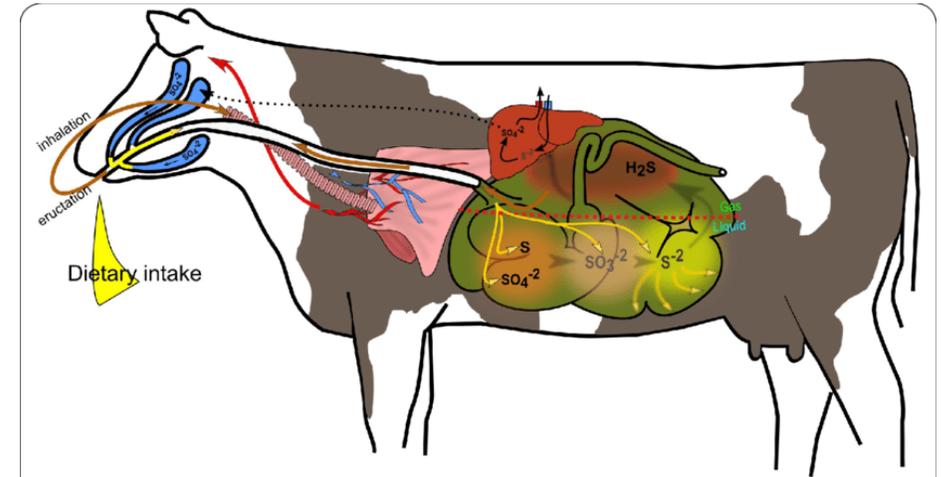
Control of rumen motility

- The forestomachs possess a rich enteric nervous system, but coordinated contractions require central input.
- Motility centers in the brainstem control both the rate and strength of contraction via vagal efferents.
- Cutting the vagus nerve in a ruminant abolishes coordinated reticuloruminal motility.
- There are also vagal afferents from the rumen to the motility centers which allow stretch receptors and chemoreceptors in the rumen to modulate contractility.
- Conditions inside the rumen can significantly affect motility. If, for example, ruminal contents become very acidic (as occurs in [grain engorgement](#)), motility will essentially cease.
- Also, the type of diet influences motility: animals on a high roughage diet have a higher frequency of contractions than those on a diet rich in concentrates.



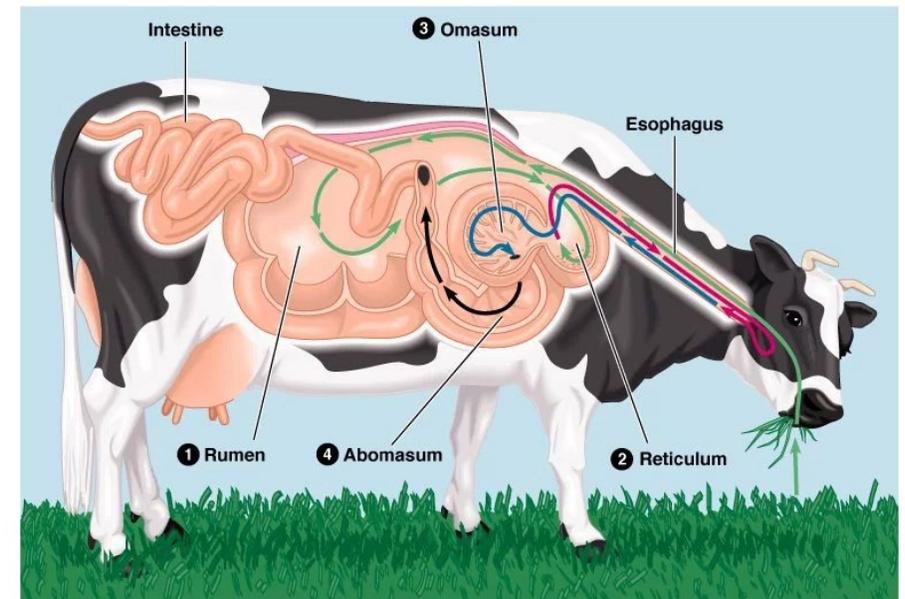
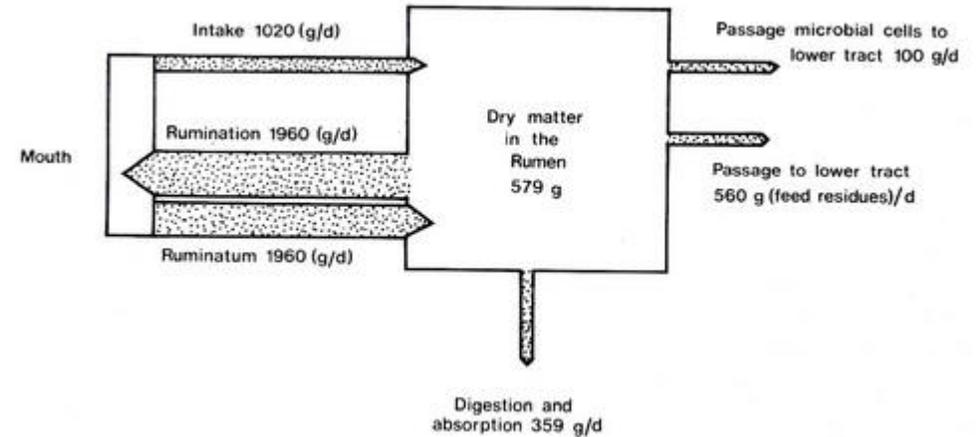
Rumination and Eructation

- Fermentation in the rumen generates enormous, even frightening, quantities of gas. We're talking about 30-50 liters per hour in adult cattle and about 5 liters per hour in a sheep or goat.
- Eructation or belching is how ruminants continually get rid of fermentation gases.
- Eructation is associated with almost every secondary ruminal contraction. Eructated gas travels up the esophagus at 160 to 225 cm per second and, interestingly, a majority is actually first inspired into the lungs, then expired.
- *Anything that interferes with eructation is lifethreatening to the ruminant* because the expanding rumen rapidly interferes with breathing. Animals suffering [ruminal tympany](#) (bloat) die from asphyxiation.
- *Rumen gases, particularly methane, are increasingly in the news because of their contribution to greenhouse gas and climate change. As with most topics that attract the attention of activists and politicians, it is somewhat difficult to obtain accurate estimates of the contribution of ruminant digestive processes to global greenhouse gas. However, data from the Food and Agriculture Organization of the United Nations indicates that ruminants are responsible for roughly 20% of global methane emissions, which equates to approximately 3-5% of total greenhouse gas production.*



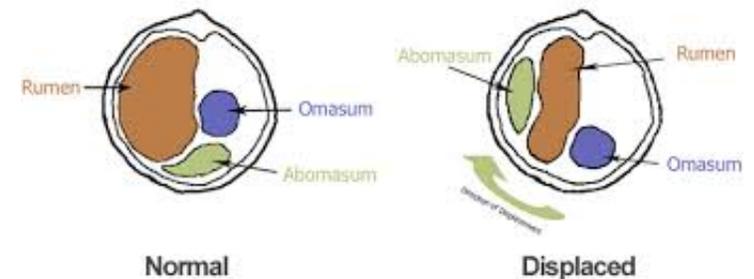
Rumination and Eructation

- Ruminants are well known for "cud chewing".
- Rumination is regurgitation of ingesta from the reticulum, followed by remastication and reswallowing.
- It provides for effective mechanical breakdown of roughage and thereby increases substrate surface area to fermentative microbes.
- Regurgitation is initiated with a reticular contraction distinct from the primary contraction.
- This contraction, in conjunction with relaxation of the distal esophageal sphincter, allows a bolus of ingesta to enter the esophagus.
- The bolus is carried into the mouth by reverse peristalsis.
- The fluid in the bolus is squeezed out with the tongue and reswallowed, and the bolus itself is remasticated, then reswallowed.
- Rumination occurs predominantly when the animal is resting and not eating, but that is a considerable fraction of the animal's lifespan.



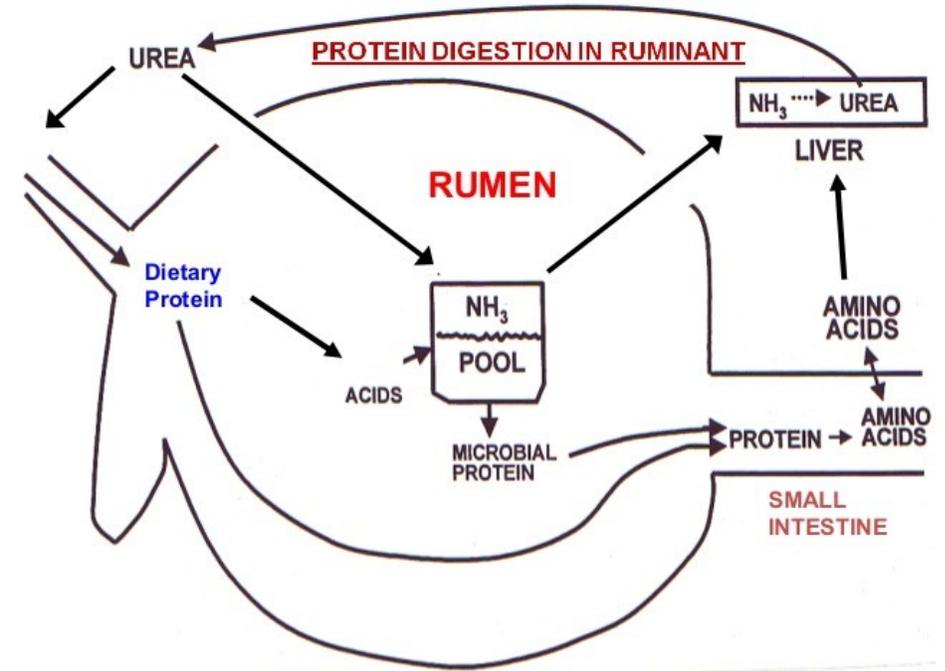
Abomasal contraction

- In ruminants, material is sent to the abomasum at a fairly steady rate.
- As with the true stomach of monogastric species, the contractions of the abomasum allow material entering the abomasum to be thoroughly mixed with the acids and enzymes of the abomasum.
- Contractions also allow some material to exit to the small intestine.
- A great amount of carbon dioxide is produced during bacterial fermentation and some remains dissolved in the rumen fluid.
- However, carbon dioxide is almost insoluble in low pH solutions and so a large amount of gas is liberated when the rumen fluid meets the acid of the abomasum.
- A unique action of abomasal contraction in ruminants is to drive gases back into the omasum and rumen for regurgitation.
- The abomasum normally contracts about 2.25 times each minute.
- It is coordinated with rumen contractions so that there are about two contractions of the abomasum for every rumen mixing contraction.
- *Unfortunately, if abomasal contractility is greatly reduced, the abomasum can fill with gas and “float” to the top of the abdominal cavity, a condition known as displacement of the abomasum. It is particularly common in dairy cows shortly after calving. It is often associated with a diet poor in fiber or a diet that promotes hypocalcemia (milk fever).*



Protein considerations

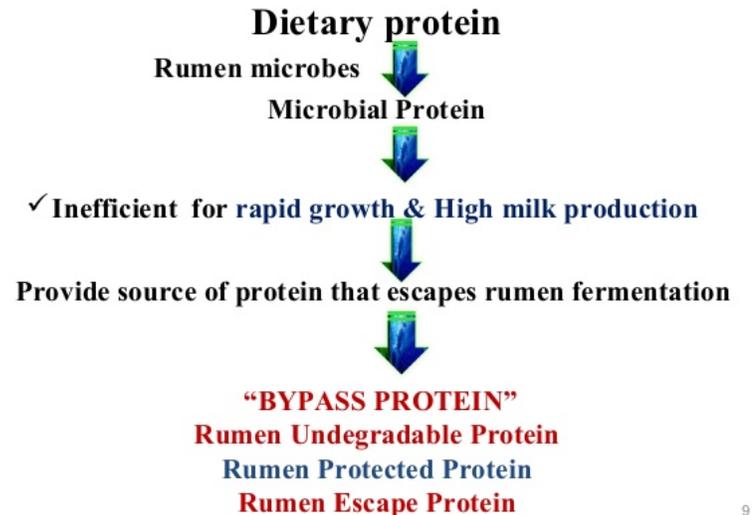
- Another possible advantage to being a ruminant is that it is possible for the rumen bacteria to provide very high quality protein to the animal.
- Rumen bacteria have the ability to combine nitrogen from ammonia or urea with carbon skeletons liberated from dietary carbohydrates to form all the amino acids that make up their protoplasm.
- When the bacteria die or move into the small intestine with other digesta, the proteins within the bacteria can be digested by mammalian proteolytic enzymes and the amino acids used by the cow.
- Microbial protein is considered very high quality: its amino acid profile is almost identical to that of muscle and milk, permitting great conversion into meat and milk by the cow.
- A disadvantage of being a ruminant is that much of the protein that is fed to the cow can be utilized by rumen bacteria.
- They find it energetically more efficient to use preformed amino acids when available rather than making them de novo. Dietary protein that the rumen bacteria can break down is referred to as rumen-degradable protein.



Protein considerations

- In monogastric animals it is critical to feed high-quality proteins to supply the animal with essential amino acids.
- In ruminants, if the protein is rumen degradable the essential amino acids are lost to the animal unless they can be recovered in the form of microbial protein that enters the small intestine.
- Not all the dietary protein fed to a cow is degraded by the rumen bacteria for their use.
- The protein that bypasses the rumen bacteria, known as rumen-undegradable protein, can be digested in the small intestine and, if it is of high quality, can be an excellent source of essential amino acids.

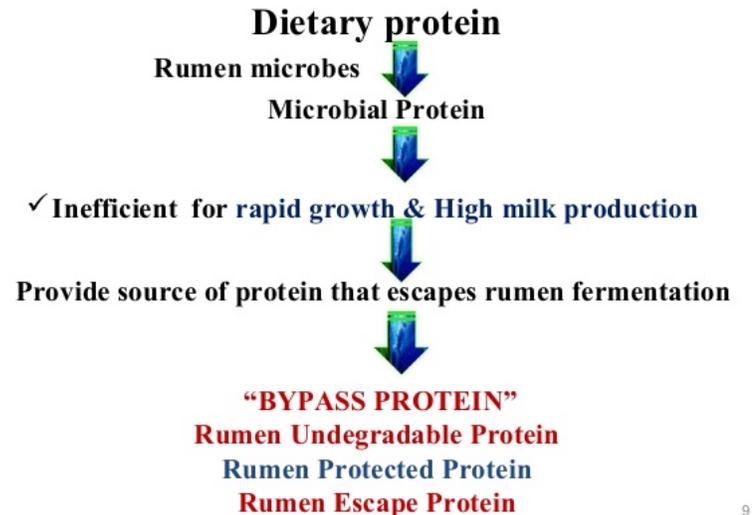
Necessity of bypass protein



Bypass protein

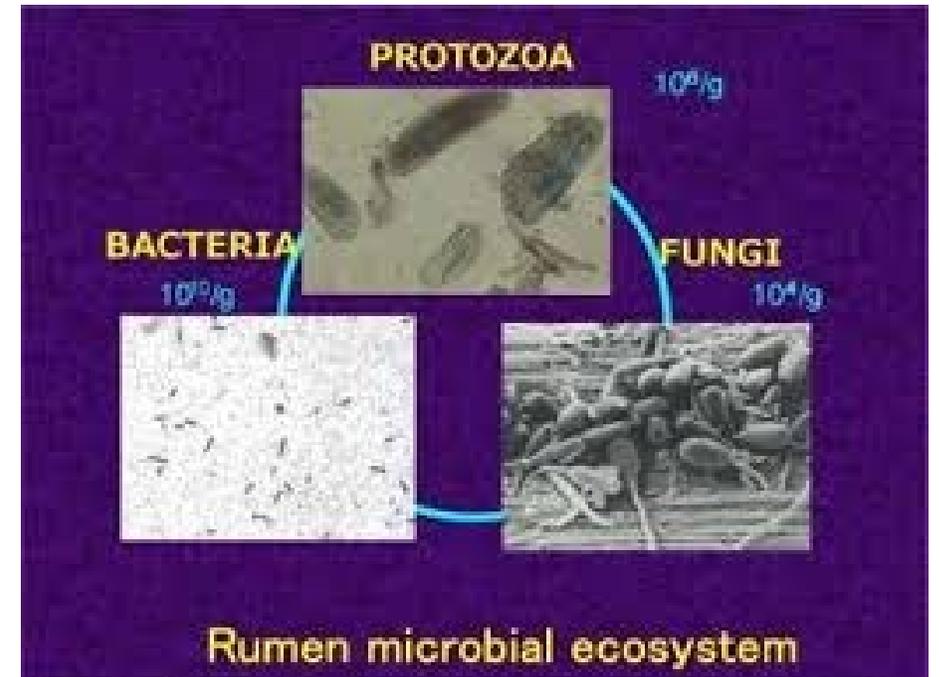
- Suckled milk for instance, is a form of both bypass protein and bypass carbohydrate (lactose).
- Both these components of milk are readily fermented in the rumen when they enter, but because of the reflex closure of the oesophageal groove while suckling these bypass the rumen and become available for digestion in the intestines.
- Bypass protein is defined as any portion of a protein meal that escapes the rumen intact and is available for digestion in the intestines
- Bypass energy (mainly starch) is that part of the feed that escapes fermentation and is digested and absorbed from the small intestine.
 - One of the costs of the ruminant mode of digestion is that fermentation of readily digestible feeds results in up to 20% of the metabolisable energy intake being lost as heat and methane.
 - A second major disadvantage is that proteins that are fermented in the rumen are lost as sources of essential amino acids.
 - In the developing countries protein is too valuable to be fermented since protein fermentation is inefficient as a source of ATP for microbial growth (about half that of an equivalent weight of carbohydrates). Also the N for microbial growth can be supplied in more elemental form (ie. as non-protein nitrogen-urea).

Necessity of bypass protein



Rumen microbial ecosystem

- The microbial ecosystem in the rumen is complex and highly dependent on diet.
- The vast majority of ruminants consume a mixture of carbohydrates, of which cellulose and hemicellulose are the largest components.
- However, at times the diet can contain large amounts of soluble carbohydrates or starch (eg. molasses or grain).
- Plants have developed molecular structures in their cell walls specifically to deter invasion by micro-organisms.
- In the rumen the main agents that break down carbohydrates are anaerobic bacteria, protozoa and fungi.
- The anaerobic bacteria are the principal agents for fermenting plant cell-wall carbohydrates but the anaerobic phycomycetous fungi may be extremely important.
- There appears to be a close relationship between fungi and the other microbes in the rumen since the fungi appear to be the first organisms to invade plant cell walls, which allows bacterial fermentation to start and to continue.
- Some rumen microbes synthesise enzymes that degrade the most complex plant structures, whilst others use only simple compounds such as cellobiose or glucose.
- Some bacteria in the rumen assume a syntropic association, where one organism uses the products of fermentation of another and the removal of the end-product allows further fermentation of the primary feed resource by the first organism.



The phycomycetous fungi

- Anaerobic fungi are probably present in all herbivorous animals and may exist in anaerobic environments such as occur in deep-sea sludges and in slurry in methane digestors.
- Sporangia protruding from the surface of plant particles release zoospores shortly after the food is consumed.
- These are able to reach newly ingested fibre and invade the tissue, usually via damaged parts of the plant or through the stomata of leaves.
- They then encyst, germinate and grow through the plant particles.
- Refractory materials, such as the leaves of wheat straw, when suspended in nylon bags in the rumen of sheep or cattle are heavily colonised by anaerobic fungi, with the areas around the leaf ribs the most densely populated.

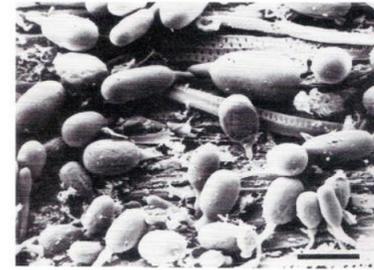


Plate 3.1 Scanning electron-micrographs of sporangia of rumen anaerobic fungi attached to lucerne stem from rumen digesta of a steer 24 hours after feeding. Bar marker = 50µm (Source: Bauchop 1985).

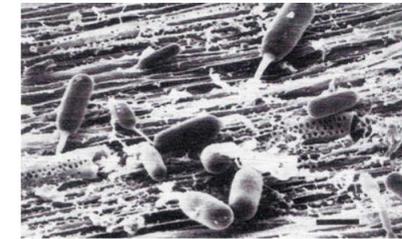


Plate 3.2 Scanning electron-micrographs of sporangia of rumen anaerobic fungi on red clover fragments from the digesta of a steer 24 hours after feeding with meadow hay. Bar marker = 50µm (Source: Bauchop 1985).

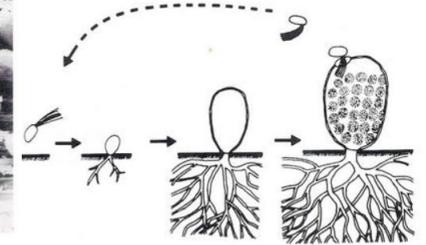


Figure 3.3 Life cycle of the anaerobic fungi in the rumen showing the release of the zoospores from the sporangia and re-infection of particulate digesta (Source: Bauchop 1985).

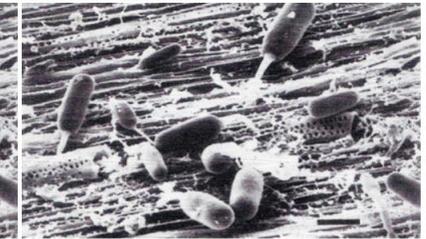
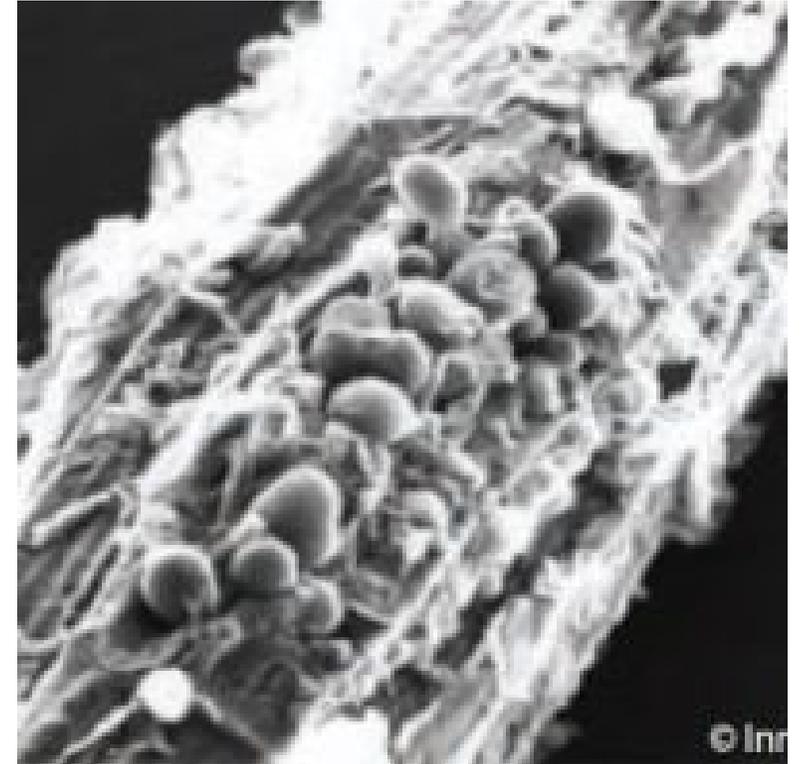


Plate 3.3 Rumen anaerobic fungi colonising wheat straw leaves that had been incubating in a nylon bag in the rumen for 24 hours. Bar marker = 50µm (Source: Bauchop 1985).

The phycomycetous fungi

- The fungi appear to be the first organisms to invade and commence digesting the structural plant components, beginning from the inside.
- They reduce the tensile strength of these particles and thus increase particle breakdown in rumination.
- **The damage to digesta particles by fungi allows bacteria to colonise the cell materials.**
- **They are thus extremely important initiators of fermentative breakdown of insoluble plant cell wall materials and their presence must reduce any lag-phase of fibre digestion.**
- The species of fungi isolated from the sheep's rumen include *Neocallimastix frontalis*, *Piramonas communis* and *Sphaeromonas communis* but more are being discovered.



Protozoa

- Protozoa occur in the rumen of sheep and cattle on fibrous diets (which are low in soluble sugars) but their population densities are low (less than 100,000/ml) whereas on diets high in starch or sugars they can reach densities of 4,000,000/ml of rumen fluid.
- The diet also determines the species of protozoa in the rumen but little is known about the factors that determine the balance of protozoal species or their biomass.
- For the purpose of this presentation protozoa are divided mainly into the small entodineomorphs (largely *Entodinia* spp.) and the large holotrich protozoa (mainly *Isotricha* or *Dasytricha* spp.)
- The former occur in animals fed starch-and/or fibre-based diets, whereas the latter have been mainly reported to occur in animals fed sugar/fibre diets (sugarcane) and on fresh grass pastures, which are usually a combination of soluble and insoluble carbohydrates.
- Some protozoa are cellulolytic but the major substrates appear to be sugars and starches, which are rapidly assimilated and stored as poly-dextran; this is mobilised as required to provide energy for the growth and maintenance of the protozoa.
- **In this way they often 'buffer' the pH of the rumen.**
- When the population of protozoa is high they may constitute up to 70% of the biomass of the organisms in the liquor with bacteria comprising only 30%.

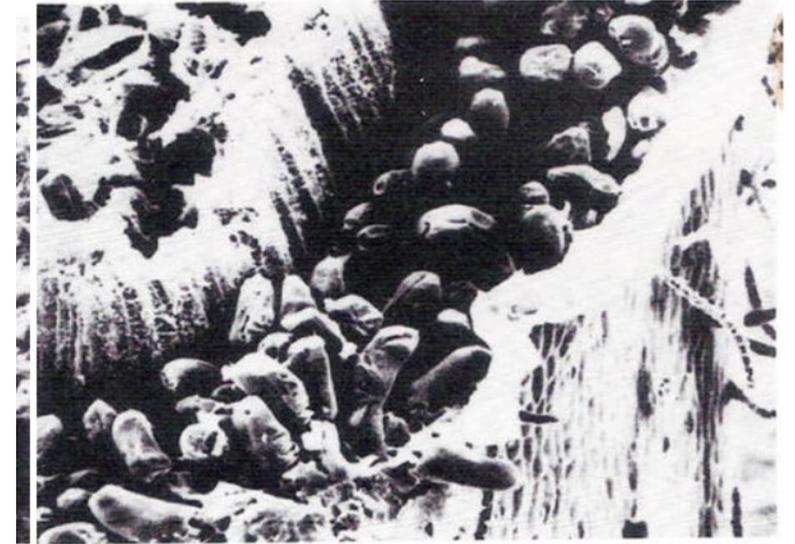


Plate 3.5 Electron micrograph of *Epidinia* spp attached to plant fibres in the rumen (reproduced with kind permission of Dr T Bauchop).

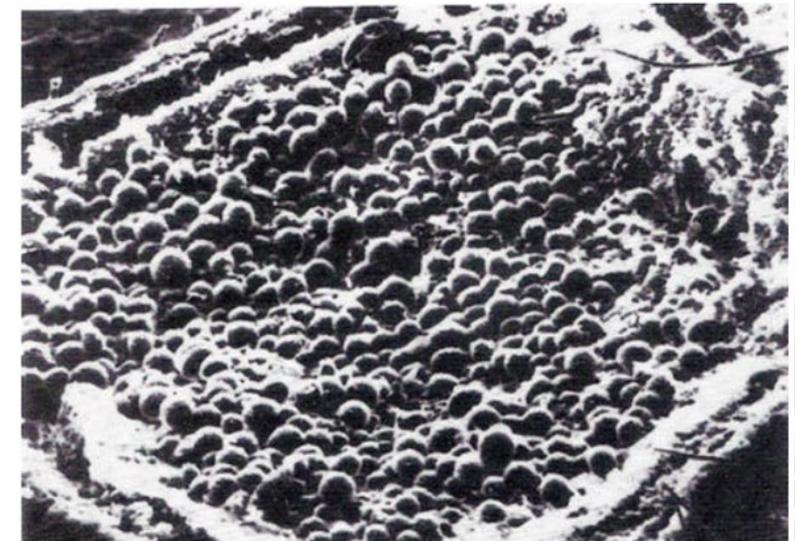
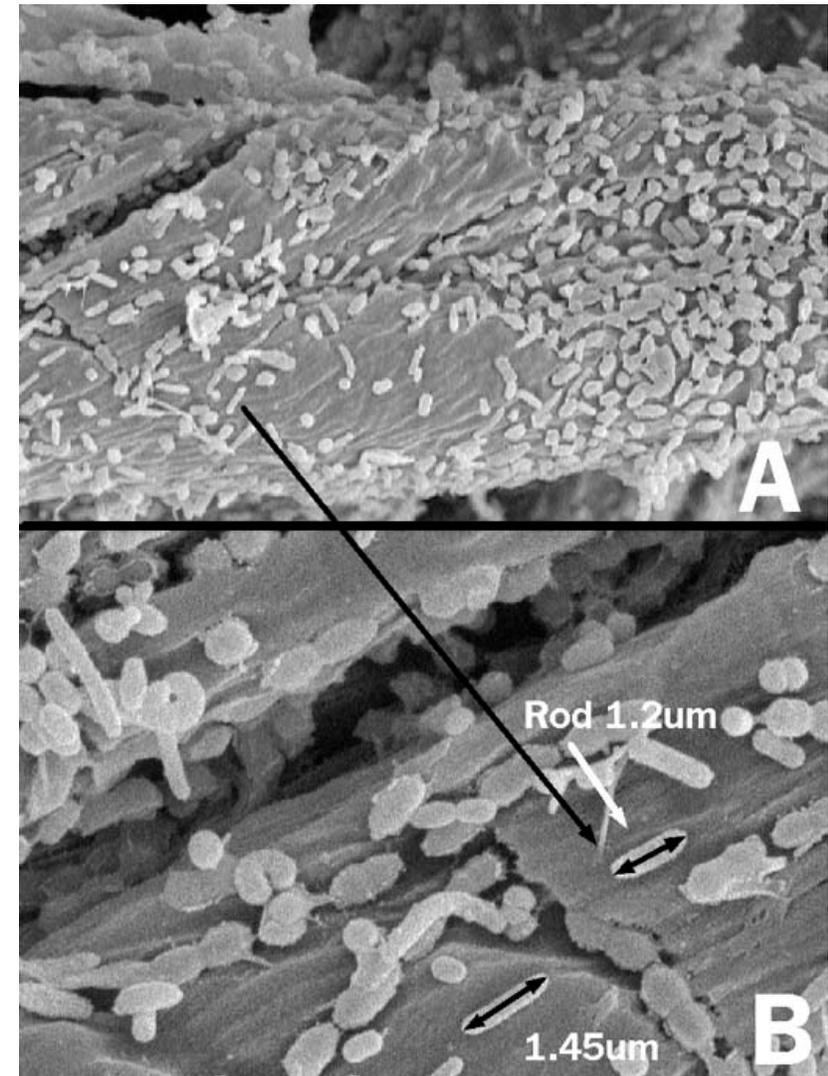


Plate 3.4 Electron-micrograph of *Dasytricha* spp attached to plant fibres in the rumen (reproduced with kind permission of Dr T Bauchop).

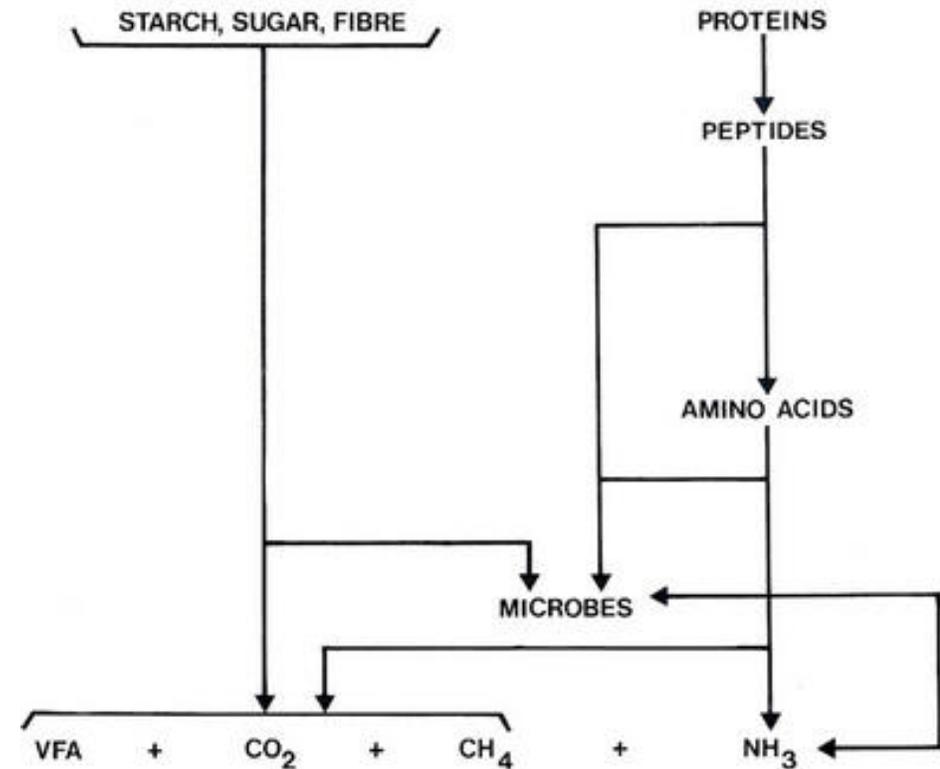
Bacteria

- Bacteria are normally the largest microbial biomass in the rumen. There are a number of distinct groupings of bacteria including:
 - Bacteria free in the liquid medium (usually 30% of the total)
 - Bacteria attached to feed particles (about 70% of the total)
 - Bacteria adhering to the epithelial lining of the rumen
 - Bacteria attached to protozoa (mainly methanogens).
- The continuous flow of particles out of the rumen necessitates that a proportion of the bacteria detach from particles that have been already largely digested, in order to colonise new material entering the rumen.
- The number of bacteria in the liquid phase is therefore important in determining the rate of colonisation and therefore the rate of fermentation of feed particles.
- The bacteria floating free in the rumen are therefore the ones that depend on soluble nutrients but there are also those that are in 'transit' between plant particles.
- The most important bacteria for fibre digestion are *Ruminococcus flavefaciens*, *Ruminococcus albus*, *Bacteriodes succinogenes* and *Butyrivibrio fibrisolvens*. In some situations *Cillobacterium cellulosolvens* and various *Clostridium* spp. become revalent.
- In general, the bacteria need to be attached in order to digest fibre, although some organisms appear to secrete extracellular enzymes.



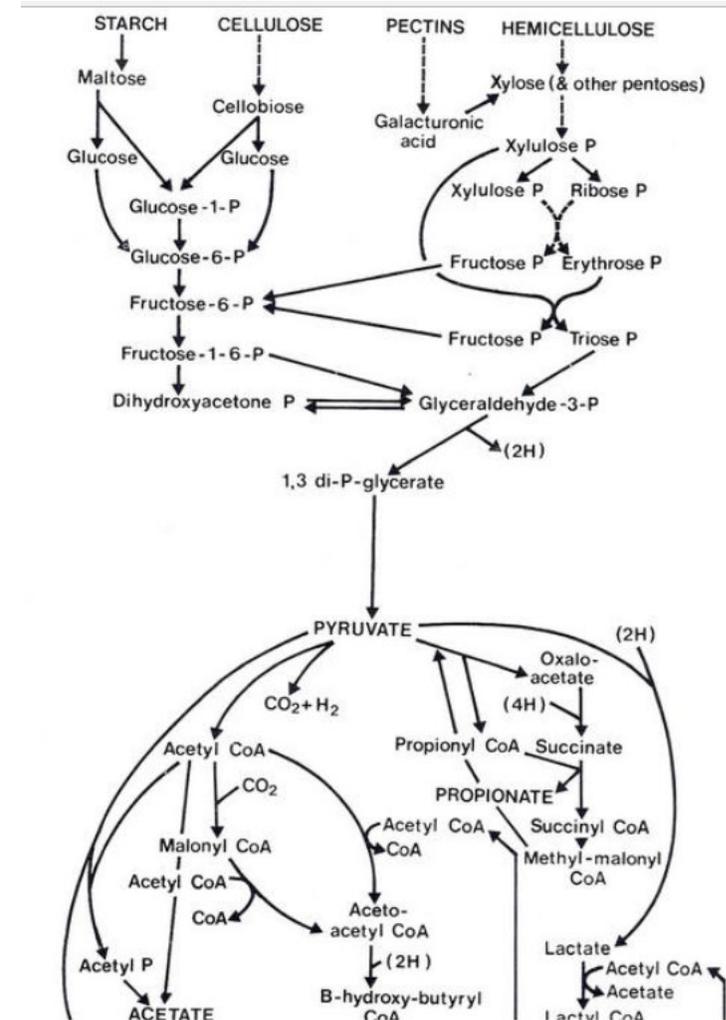
Energy transactions in the rumen

- The universal end-products of fermentation of all diets in the rumen are the VFAs (acetate, propionate, butyrate), carbon dioxide and methane.
- Energy is lost as both heat and methane.
- The ATP produced by conversion of feed to VFAs and intermediary compounds used in cell growth is the main source of energy for the growth of micro-organisms.



Energy transactions in the rumen

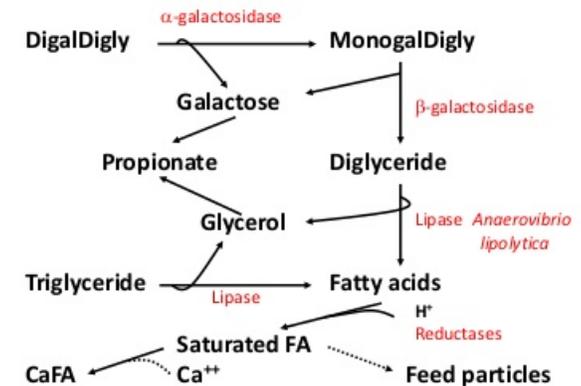
- The diagram shows that the digestible components of ingested feed are:
 - Converted to VFAs
 - Broken down to intermediate components that are the monomers for microbial growth
 - Avoid fermentation and move to the lower digestive tract where they may be digested.



Fate of dietary fat in the rumen

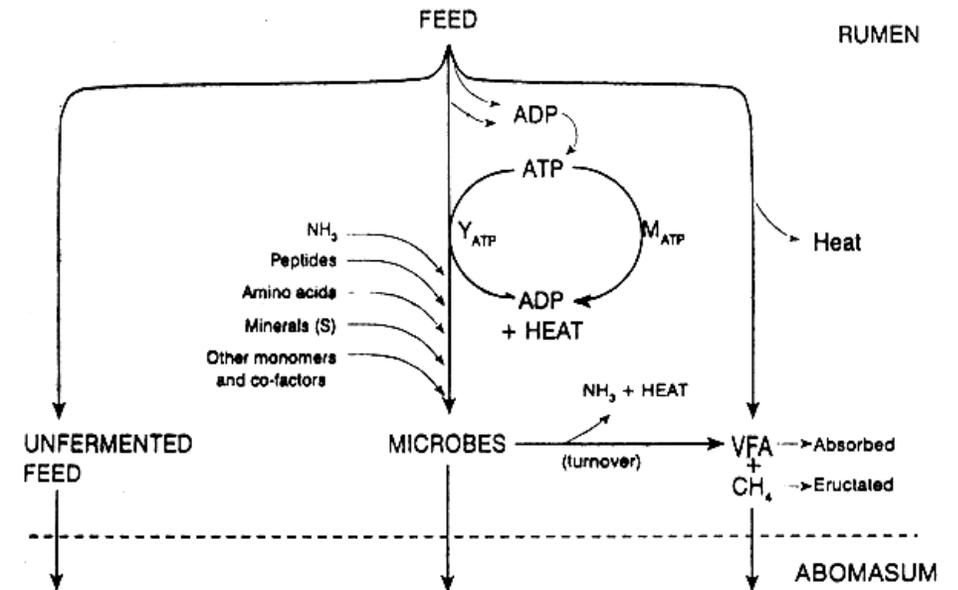
- Fat in the diet of ruminants varies from negligible amounts to levels in excess of 10% of the dry matter in leafy forages or where animals are able to select leaf-tip materials.
- Most of the lipids in pasture plant materials are phospholipids and glycolipids.
- The major long-chain fatty acid components of these are linolenic (50%), linoleic (10%) and palmitic (15%).
- The complex lipids of plants are rapidly hydrolysed in the rumen by bacterial lipases to fatty acids, galactose and glycerol; the last two are fermented to volatile fatty acids.
- The long-chain fatty acids are largely unsaturated and as soon as they are released they are adsorbed onto particles in the rumen where they are hydrogenated by microbes.
- These long-chain fatty acids (now largely stearic, palmitic and oleic acids) are absorbed only from the intestines.
- Rumen bacteria incorporate some of the long-chain fatty acids into their cellular components.

Lipid digestion in rumen



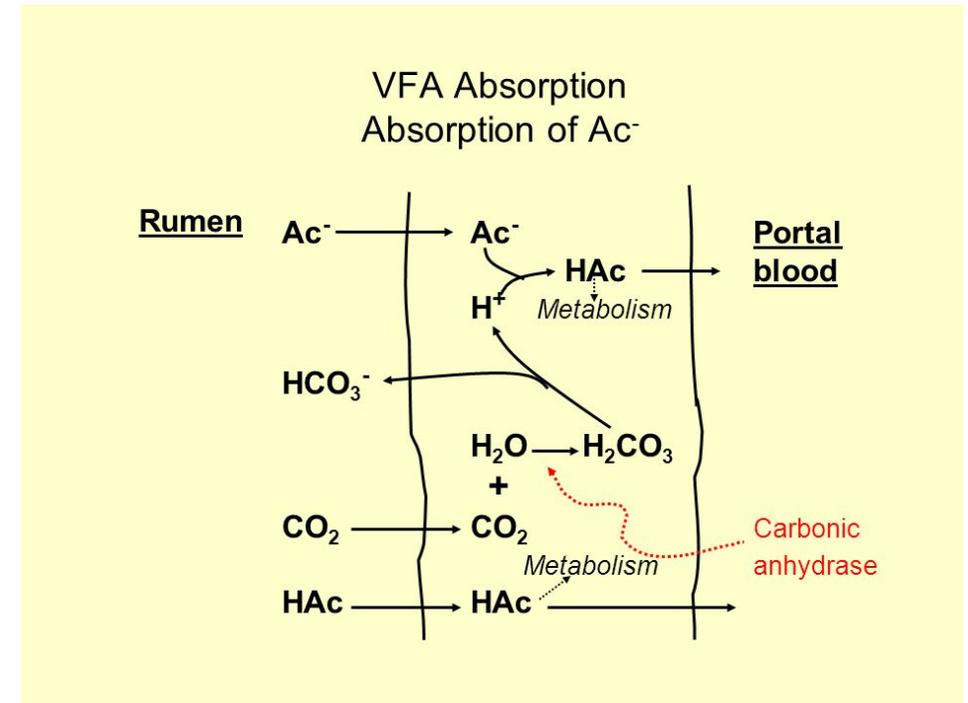
Microbial growth and fermentation

- Anaerobic conditions of the rumen limit the availability of ATP for microbial growth.
- In aerobic microbial systems the carbohydrate is converted to carbon dioxide and water with a yield of 36 moles ATP/mole of glucose oxidised.
- By contrast, anaerobic fermentation yields only about 4 moles ATP/mole of glucose converted to VFAs.
- **Rumen micro-organisms use ATP for essentially two purposes:**
 - For the energy to synthesise their own cells
 - To provide the energy for maintenance.
- The ATP available for microbial growth depends on that required to maintain the organisms.
- The efficiency of ATP generation and cell growth also depends on the substrates that provide the 'building blocks' of the micro-organisms.
- The composition of bacterial cells is fairly uniform and the cost (in ATP terms) of synthesis of the individual components of cells can therefore be calculated



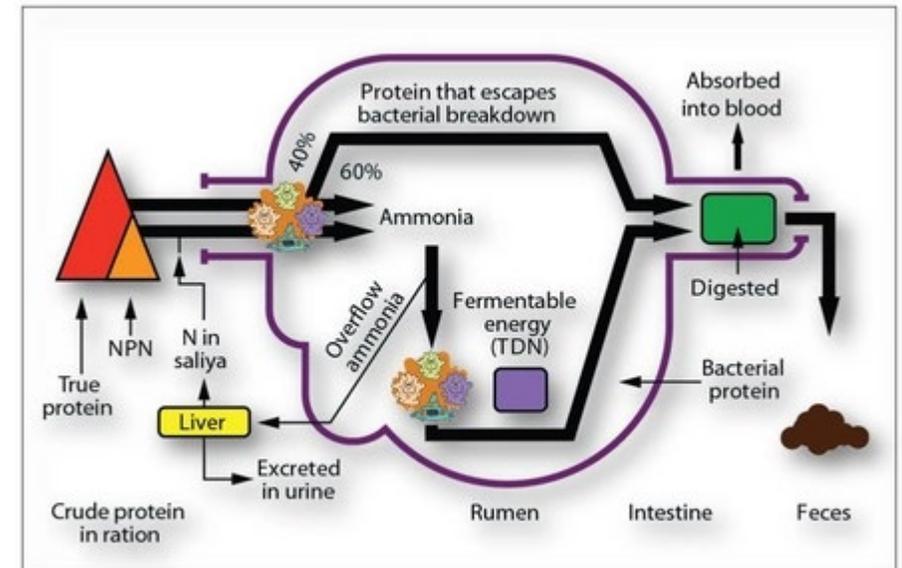
Absorption of volatile fatty acids across the rumen wall

- VFAs are absorbed from the rumen, apparently by diffusion across the rumen wall.
- About 25% of the VFAs are absorbed from the post-ruminal tract since they leave the rumen in the digesta.
- A large proportion of the fluid from the reticulum passes unchanged to the abomasum by way of the omasal sulcus but most of the water and electrolytes (particularly bicarbonate ions) are absorbed from the omasum.
- The VFAs are metabolised in the epithelial wall of the rumen and omasum
- **Since the absorption of VFAs from the rumen appears to be by simple diffusion, the requirements for substrate of the rumen wall are mainly to meet (i) the energy requirements for active transport of electrolytes and (ii) the maintenance energy requirements for the turnover of the tissue and the replacement of worn-off rumen epithelium.**
- **The individual VFAs are metabolised by the rumen epithelium. A proportion of the acetate is oxidised to CO₂; propionate is oxidised to CO₂ but, contrary to previous suggestions, little or no conversion to lactate occurs. Butyrate is oxidised to CO₂ and converted mainly to ketone bodies.**
- Propionate is removed almost totally from blood by metabolism in the liver.
- Propionate contributes extensively to glucose synthesis and possibly produces 80-90% of the glucose synthesised.
- The formation of B-hydroxybutyrate together with acetate, which pass unchanged through the liver, conserves substrate for oxidation in extrahepatic tissue.
- The liver probably obtains its substrates from propionate and butyrate and it may also remove some of the long-chain fatty acids that are absorbed from the digestive tract.



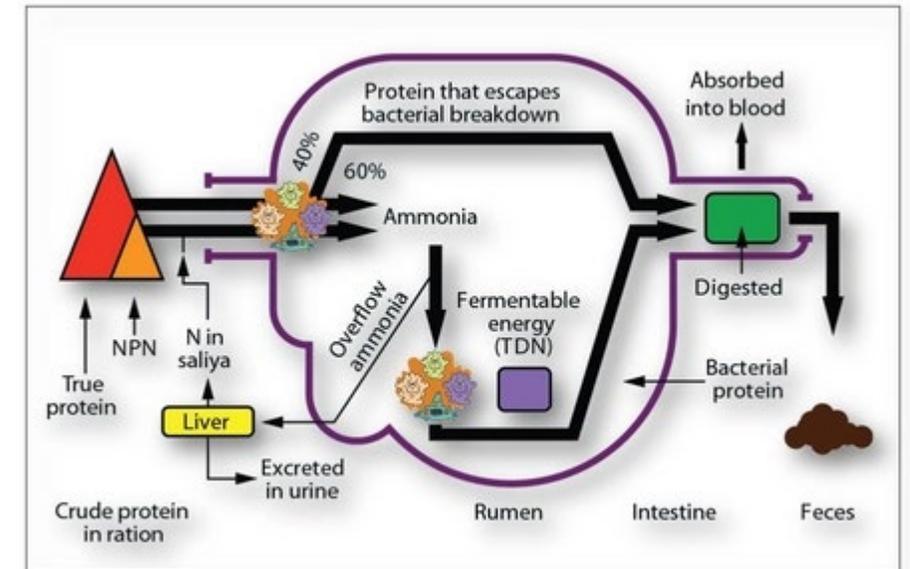
N-transactions in the rumen

- **Dietary nitrogen**
- In the industrialised countries, only relatively small amounts of urea are fed to ruminants and protein provides most of the dietary nitrogen.
- The non-protein-nitrogen fractions of such feeds include amides, amines, amino acids and nitrate; the last mentioned may be present in significant quantities in immature pasture.
- **Degradation of dietary protein in the rumen**
- Between 20 and 100% of the protein in many diets based on high-protein forages, protein meals and grains may be soluble.
- It is assumed, for practical purposes, that the solubility of protein-N in buffer solution indicates the degradability of the protein of a meal in the rumen.
- However, soluble proteins such as serum albumin, ovalbumin, chloroplast protein extract and soluble proteins from soya bean meal and rapeseed meal have variable resistance to degradation in the rumen.
- Degradation of protein to peptides and amino acids is by bacterial (usually surface) proteases and peptidases.
- Fermentation of particulate proteins depends on the length of time that they are in the rumen, and factors such as their rates of solubilisation and enzymatic degradation.
- In addition to chemical factors affecting rates of degradation of soluble proteins (ie. cross-linking and number of accessible hydrolysable sites in the protein molecules, enzyme concentration, and pH), physical characteristics of particles also affect accessibility of proteins to enzymatic action.



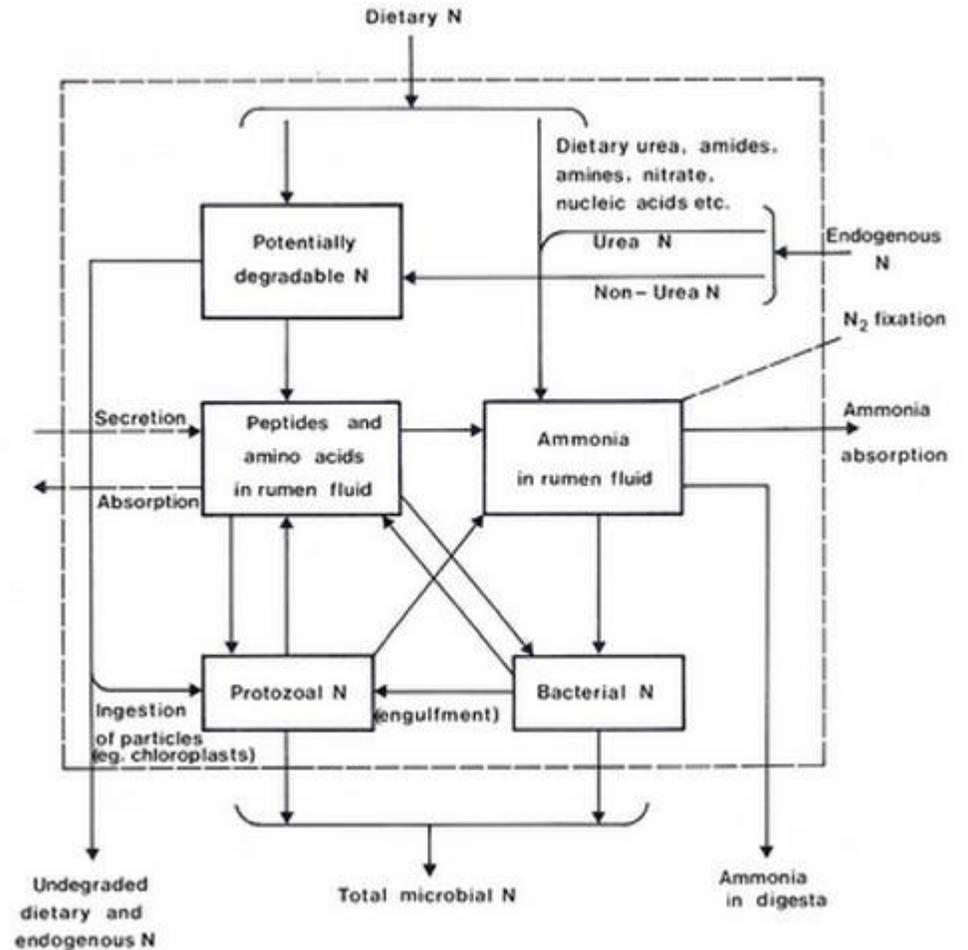
N-transactions in the rumen

- **Outflow of dietary and endogenous nitrogenous materials from the rumen**
- The amount of dietary N leaving the rumen is determined principally by the total N in the diet, the rate of its fermentation and its residence time in the rumen.
- **Peptides and amino acids in rumen fluid**
- In animals fed high-protein diets, a high proportion of the N in the rumen may be derived from peptides and amino acids in the feed protein.
- Peptides or amino acids are degraded rapidly by bacterial peptidases and deaminases, and peptides are present in the rumen in significant quantities only when the protein is fermented at high rates.
- Amino acids are absorbed from the rumen but probably only in small amounts as the majority of free amino acids are probably deaminated to give rise to branched-chain volatile fatty acids (VFAs), carbon dioxide and methane.



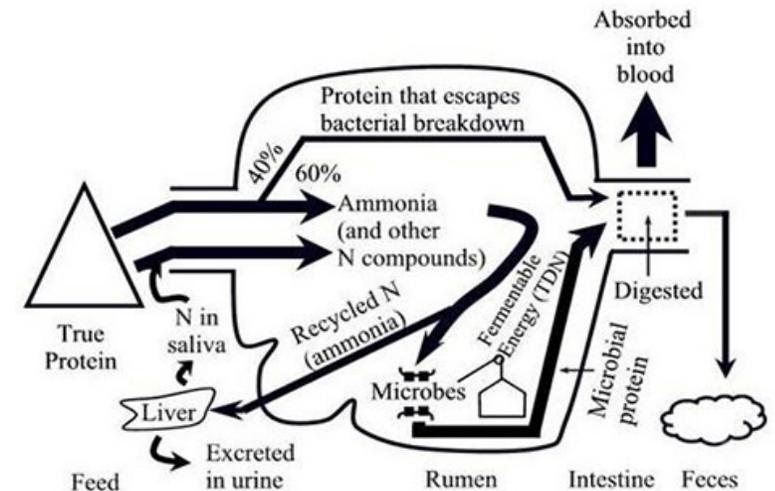
N-transactions in the rumen

- **Rumen ammonia pool**
- The sources of ammonia in the rumen include proteins, peptides and amino acids (see preceding section), and other soluble-N materials. Urea, uric acid and nitrate are rapidly converted to ammonia in the rumen. Nucleic acids in rumen fluid are probably also degraded extensively to ammonia.
- Ammonia N is lost from rumen fluid by:
 - Incorporation into microbial cells that pass out of the rumen
 - Absorption through the rumen wall
 - Passing out of the rumen in fluid.
- The ammonia pool in the rumen is relatively small and turns over rapidly. The amount of ammonia entering the pool varies over a wide range according to quantity and degradability of protein in the diet and with the extent and method of supplementation of urea. Concentrations of ammonia N in the pool can be expected to change rapidly even when animals have continuous access to food.
- To maintain a high level of ammonia in rumen fluid over 24 hours on low-protein diets requires urea to be taken in continuously.
- This can be ensured by spraying urea on the basal feed or by providing a urea block or liquid mixture which is licked at regular intervals.
- Urea given in a single meal is unlikely to maintain rumen ammonia levels above the minimum required for efficient fermentation for more than a few hours per day



Recycling of N to the rumen from plasma urea

- Rumen microbes break down most protein consumed and ammonia is produced as a by-product.
- Ammonia can be utilized in one of two ways. Microbes can use it to form microbial protein or, if ammonia levels exceed the microbes' ability to utilize it, ammonia is absorbed into the blood stream where it is carried to the liver.
- The liver detoxifies ammonia and converts it into urea to be excreted into urine.
- A portion of urea is recycled back to the rumen through saliva.
- Enzymes in the rumen rapidly break down urea back into ammonia which can then be used by microbes or absorbed.
- *Rumen microbes use ammonia as a part of their diet. It doesn't matter if it originates from true protein or NPN. Other necessary nutrients for microbial growth are carbohydrates and minerals. It is essential that ammonia be released simultaneously with available energy for ammonia to be converted into microbial protein. Also, phosphorus, sulfur and trace minerals must be present within the rumen environment in order for microbes to manufacture essential amino acids. The cow receives beneficial protein for its own needs when the bacteria and protozoa pass from the rumen to the abomasum and intestines where the microbes themselves are digested.*



THANK YOU

