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Write your answers in your notebook.

6

The Gastrointestinal Tract and Nutrition

Key Terms

Abomasum
Anaerobic
Bacteria
Bolus
Carbohydrates
Carnivore
Cecotrophy
Cellulase
Cellulose
Chyme
Colic
Coprophagy
Defecation
Deglutition
Denature
Digestion
Duodenum
Enzymes
Eructation
Fermentation
Forestomachs
Herbivore
Ileum
Jejunum
Mastication
Micturation
Monogastric
Omnivore
Papillae
Peristalsis
Prehension
Protein
Protozoa
Proventriculus
Rumen
Ruminal bloat
Ruminant
Rumination
Salivation
Symbiosis
Vitamin
Volatile fatty acid (VFA)

Learning Objectives

After you have studied this chapter, you should be able to:

- Describe the methods of the breakdown of food.
- Classify digestive systems according to stomach type and type of diet consumed.
- Describe the steps of digestion.
- Identify the differences and similarities in the digestive processes of animals.
- Explain the importance of the complex stomach of the ruminant and its benefits to the animal.

INTRODUCTION

Feeds and feedstuffs are chemically complex mixtures of substances that contain the nutrients an animal needs. The digestive tract breaks down those complex materials to their constituent parts so the nutrients can be absorbed and metabolized by the body. Breakdown of food by the digestive system in preparation for absorption is called **digestion** and is accomplished in three ways: (1) the physical or mechanical actions of chewing (mastication) and muscular action of the digestive tract (peristalsis); (2) the chemical action of hydrochloric acid, which is used by the stomach to denature proteins and bile used in the small intestine to help digest fats; and (3) the action of enzymes, which increase the speed of the breakdown of the chemical bonds in foods by the addition of a

Digestion The physical, chemical, and enzymatic means the body uses to render a feedstuff ready for absorption.

Enzymes Proteins capable of catalyzing reactions associated with a specific substrate.

water molecule (hydrolytic enzyme). **Enzymes** can be produced by the digestive tract and accessory organs (liver, pancreas), or by microorganisms living in symbiosis with the animal. Enzymes are biological catalysts that speed the rate at which a particular reaction reaches equilibrium. Many enzymes are found in the system and are needed for faster and more efficient digestion.

One of the intriguing things we know about nutrient metabolism and the metabolic pathways for different species is that they are essentially the same. *E. coli* and giraffes have much the same thing happening at the cellular level. However, they have different nutrient requirements, consume different types of feed, and digest food very differently. This difference in digestive types has allowed dissimilar species to fit into different places in the food chain and carve a niche for themselves. The type of digestive system an animal has dictates what the animal can successfully use as feed. The more complicated the feed (like forage), the more complicated the digestive tract. Thus, the ruminant system is designed to retain feed for several days, which is a long time compared to the few hours that a feed is held in a carnivore's simple tract (Figure 6–1).

CLASSIFICATION OF DIGESTIVE SYSTEMS

Monogastric Having only one stomach. Also, nonruminant.

Ruminant Hooved animals that have a rumen and chew their cud.

We classify the different digestive systems anatomically by the type of stomach an animal has. **Monogastrics,** or nonruminants, are one-stomached, or simple-stomach, animals. They can have a very simple tract, as in the mink and dog, or a cecal digestion, as in the horse, rabbit, or rat. Monogastrics that have a cecal fermentation can use much more fibrous feedstuffs than can a simple monogastric. Others, like the kangaroo, rely on a sacculated stomach to retain fibrous material for better digestion. The **ruminants**—cattle, sheep, goats, and pseudoruminants (llamas)—are more complex-stomached animals that have more than one stomach compartment. These compartments are located before the true stomach. A complicated fermentation takes place there to help the animal make use of fibrous feeds. These tracts usually also have a cecum, which helps to retain the feed even longer.

Carnivore An animal that subsists on meat.

Omnivore An animal that selects a diet of both plant matter and meat.

Herbivore An animal that eats a diet of only plant material.

Cellulase An enzyme that specifically attacks and digests cellulose.

Cellulose A carbohydrate composed of thousands of glucose molecules that forms the support structure of plants.

Prehension The act of seizing and grasping.

We also classify digestive systems according to the type of diet the animal normally consumes. There are three digestive categories based on diet. **Carnivores** are flesh-eating animals, for example, cats and birds of prey. **Omnivores** eat both animal and vegetable matter; examples include chickens, pigs, and humans. **Herbivores** eat vegetable-based feeds. They are able to digest this plant material with the help of **cellulases** provided by bacteria during the fermentation process. Horses, cows, rabbits, guinea pigs, llamas, kangaroos, elephants, and many others are herbivores. All herbivores have some specialized way to help them digest **cellulose**.

AN OVERVIEW OF THE STEPS OF DIGESTION

Prehension, the means an animal uses to bring food into its mouth, is the first step of digestion. Animals use a variety of prehension methods, including use of their upper limbs, head, beak, and claws, and their mouth, teeth, and lips. Herbivores use the tongue, teeth, or lips to grasp forage. Ruminants have no upper incisor teeth, therefore the cow uses its flexible tongue to bring forage into its mouth and cuts the forage off with the lower incisor teeth and upper dental pad. Sheep use their teeth and cleft upper lip to permit them to graze close to the ground, which can lead to overgrazing. Horses make use of their mobile, prehensile upper lip, as well as upper and lower incisor teeth.

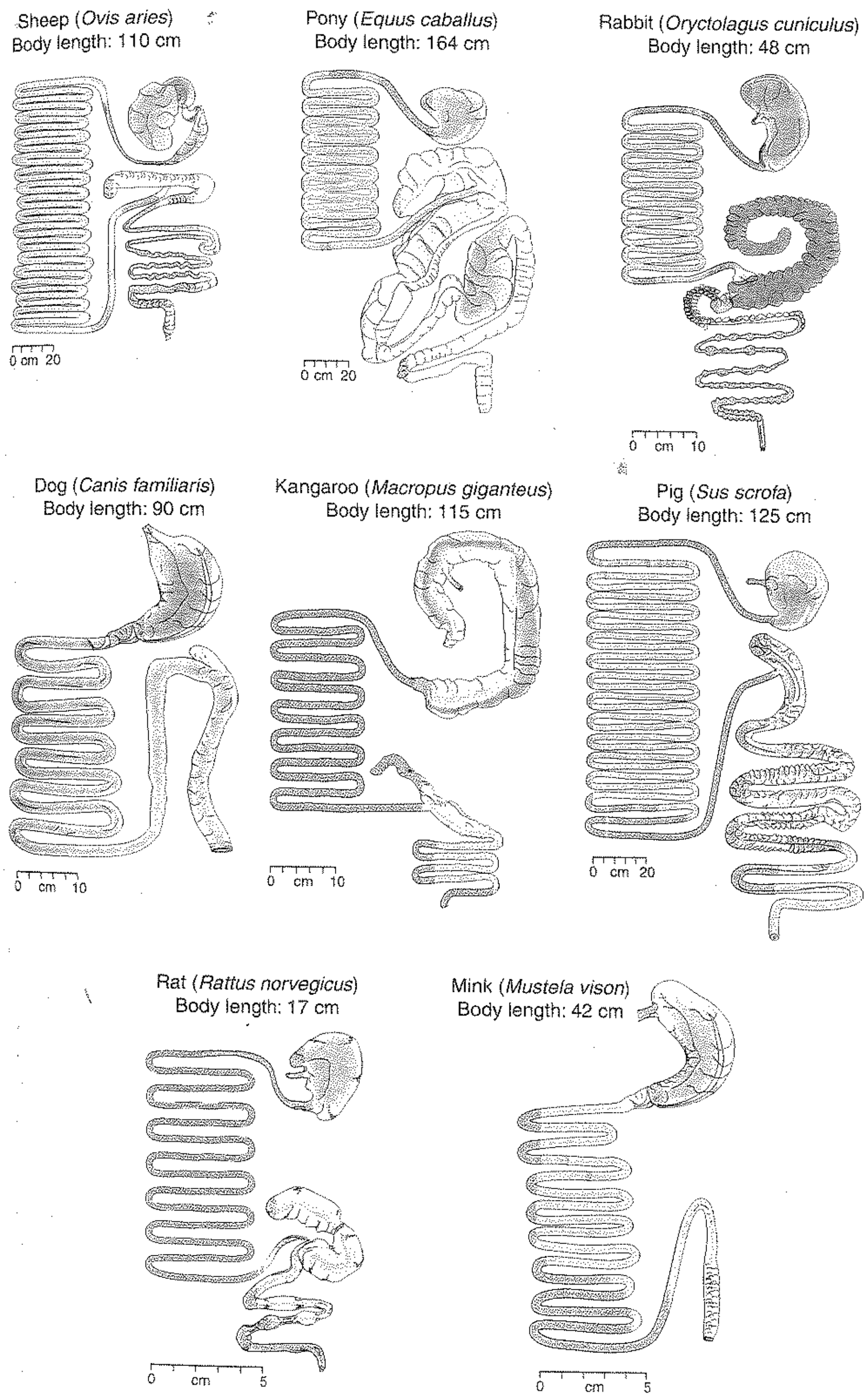
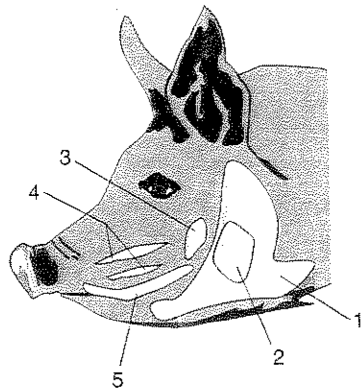


Figure 6–1
Mammalian digestive tracts.
(Source: Swenson, 1984. Used by permission of the publisher, Cornell University Press.)

Mastication, or chewing, involves the vertical and lateral action of the jaw and teeth to crush food. Carnivores chew only to the extent needed to reduce the size of their meat so it can be swallowed. All herbivores need thorough mastication of their feed, mostly forage, to allow bacterial enzymes access to the cellulose. Ruminants first form a bolus and then swallow it without much chewing. Later they regurgitate the feed and thoroughly chew it. This process is one of the key elements

Mastication The process of chewing.

Figure 6–2
Salivary glands of the pig.



Rumination The process in ruminants where a cud or bolus of rumen contents is regurgitated, remasticated, and reswallowed for further digestion.

Salivation The elaboration of the mixed secretion (saliva) produced primarily by three bilateral pairs of glands in the mouth known as salivary glands.

Ruminal bloat More correctly called *ruminal tympany.* An overdistention of the rumen and reticulum with the gases of fermentation. Commonly referred to as *bloat.*

Deglutition The act of swallowing. Passing material from the mouth through the esophagus to the stomach.

Bolus A rounded mass ready to swallow.

Peristalsis The progressive squeezing movements produced by the contraction of muscle fibers found in the wall of the digestive tract.

of **rumination.** A typical dairy cow chews between 40,000 and 50,000 times a day. Cecal fermentors and some simple monogastrics must chew thoroughly before swallowing because the food goes directly into the glandular stomach for digestion. They don't regurgitate their feed.

Salivation includes secretion and mixing of saliva with food. Three main paired salivary glands produce saliva (Figure 6–2). These are the parotid (below the ear), the submaxillary (mandibular) (at the base of the tongue), and sublingual (under the tongue). Saliva is mixed with food during chewing and has many functions. The first function is to lubricate food so the animal can chew and swallow it. All animals depend on this most irreplaceable salivary function. Both the water content and the protein mucin, found in saliva, are responsible for the lubricating function. Think how hard it would be for you to eat a cracker or for herbivores to eat forage without saliva. The solvent action of saliva dissolves small portions of food, allowing it to come into contact with taste buds, and gives food its taste. Saliva may also stimulate the taste nerves. The washing action of saliva cleanses the mouth and prevents decay of leftover food particles. The enzyme lysozyme supplies a disinfectant action that kills bacteria that could harm teeth and gums. Dogs and other carnivores have especially large amounts of lysozyme. Ruminants rely heavily on the bicarbonates in saliva to buffer the acids produced by the microorganisms in the rumen. The acids would soon damage the rumen wall if they weren't buffered. Saliva provides readily available nutrients for rumen microorganisms and helps maintain the proper pH for the microorganisms. Mucin, which is a protein, is digested and used by the microorganisms once it reaches the lower tract. Urea is harvested from the blood by salivary glands and secreted with the saliva. The microorganisms use it to manufacture protein. Salivary phosphorus (P) and sodium (Na) are also used by the microorganisms. The antifrothing property of saliva helps prevent **ruminal bloat** from being a daily occurrence. It prevents formation of a stable foam that would interfere with eructation (belching). Saliva also has an excretory function.

Swallowing, or **deglutition,** is the passing of food and water (or anything else) from the mouth to the first stomach compartment via the esophagus. The swallowing reflex is involuntary and under neural control. It is caused by the presence of material in the back of the mouth. The tongue is responsible for forming a **bolus** of the food in the mouth and voluntarily pushing it to the back of the mouth. Muscle contractions (**peristalsis**) move the food to the stomach. The cardiac valve is a valve located at the end of the esophagus that prevents feed in the stomach from coming back into the esophagus in some species.

In the ruminant, the feed makes its first stop in the rumino-reticulum for fermentation. Fermentation is an important topic and discussed at length later in this chapter. In the monogastric, the first stop is in the true stomach, which represents the next stop after the forestomachs for the ruminants.

Significant chemical and enzymatic digestion begins in the glandular stomach, which is similar in most animals. In the chicken, the stomach is called the **proventriculus,** and in the cow, it is called the **abomasum**. Physical breakdown of food occurs because of the churning action created by the contractions of the strong stomach muscles. The churning action also mixes the food (ingesta) with chemicals and enzymes. Chemical digestion is provided by hydrochloric acid (HCl), which is secreted by gastric glands in the stomach. HCl **denatures** proteins, a crucial first step in their digestion. In the native state, proteins are poorly digested. In denatured form, enzymes readily hydrolyze them. HCl activates the enzyme pepsin from its precursor pepsinogen. HCl provides an acidic pH in the stomach that is needed for gastric enzymes to work. HCl kills bacteria, which renders the stomach almost sterile. Several enzymes secreted in the stomach gastric juice provide enzymatic digestion of food. These include pepsin, gastricin, and rennin, all of which work on proteins. Rennin hydrolyzes the milk protein casein. This enzyme is not important in the adult animal, but it is especially important in young ruminants. Gastric lipase acts on fat.

Proventriculus The glandular stomach in fowl.

Abomasum The true glandular stomach in the ruminant.

Denature In protein chemistry, to disrupt the structure of a native protein causing it to lose its ability to perform its function.

In addition to digestion, the stomach stores food, another important function. This allows the animal to eat at a much faster rate than if digestion had to occur as rapidly as the food was consumed. The food is then metered into the lower gut as it is capable of digesting it.

The small intestine is divided into three portions. The **duodenum** is the first part. It extends from the pylorus of the stomach to the beginning of the jejunum. In most species, the duodenum is in the form of a loop and is often referred to as the duodenal loop. It is generally only about 1 ft long. Bile and pancreatic secretions enter in this portion of the small intestine. Excluding microbial fermentation, the duodenum is the main site of food breakdown in the entire digestive system. The **jejunum** is the second and longest part of the small intestine. Digestion continues here, but its major function is the absorption of digestive end products. The jejunum is several feet long. The **ileum** is the third part. Its major job is to form the connection to the large intestine, but absorption occurs here also. The entire small intestine is lined with **mucous membranes**. There are folds within this layer that serve to increase the surface area considerably. The jejunum portion of many species is covered with microscopic villi, which may number in the millions. They increase the absorptive surface tremendously. Nutrients are absorbed into the villi and pass into the lymphatic system or the circulatory system. Carbohydrates, amino acids, short-chain fatty acids, water-soluble vitamins, and most minerals absorbed from the small intestines enter the bloodstream. They go first to the liver and then are distributed to the rest of the body. The rest of the lipids and fat-soluble vitamins are transported by the lymphatic system to the thoracic duct, and they empty into the vena cava to be further transported.

Duodenum The first segment of the small intestine.

Jejunum The second and longest portion of the small intestine.

Ileum The last short portion of the small intestine.

Mucous membrane Cell layer covered in epithelial cells that both absorb and secrete.

The small intestine is the chief site of food digestion and nutrient absorption for monogastrics. When **chyme** leaves the stomach, it is very acidic. Chyme is mixed in the duodenum with three alkaline secretions, all very important to digestion. These secretions are bile, pancreatic juice, and succus entericus. Bile is formed in the liver. It is concentrated (up to 20 times for some species) and stored in the gallbladder until needed for digestion. Some species, like the rat and horse, don't have a gallbladder. Because they eat many small meals throughout the day, they secrete bile continually. Bile salts, which are derivatives of cholesterol, assist in the digestion and absorption of fats.

Chyme The name given to the material consisting of food, saliva, and gastric secretions.

Pancreatic juice, the second alkaline secretion of importance, contains the really important, very potent digestive (hydrolyzing) enzymes. In hydrolysis, a compound is split into two or more simpler compounds by the uptake of the H and OH parts of a water molecule on either side of the chemical bond cleaved. The main enzymes are trypsin, chymotrypsin, carboxypeptidase, aminopeptidase, intestinal lipase, and amylase.

The third secretion, succus entericus (intestinal juice), is secreted by glands in the small intestine itself in large amounts. For example, a human may secrete 20 liters per day. Its function is to lubricate, dilute, and increase the pH of the food mixtures.

Relative capacities of the large intestine and ceca vary greatly from species to species. Monogastric herbivores have the large intestine of greatest relative volume and carnivores have the smallest. The large intestine contains no villi; thus absorption is restricted. Mucous glands line the large intestine to provide lubrication. Note that no digestive enzymes are secreted in the large intestine by the animal. Any enzymes found there must be left over from secretions found earlier in the tract or are provided by microorganisms. The large intestine has three parts: colon, cecum, and rectum. The material that enters from the small intestines is liquid and contains cells, undigested foodstuffs, and digestive secretions. Water, electrolytes, vitamins, minerals, and volatile fatty acids (VFAs) are absorbed from this material, with emphasis on water and electrolytes. The contents of the large intestine are not sterile. The feces contain about 50% bacteria by weight. A variety of bacteria grow in feces, the most common being coliform bacteria (fecal bacteria). These bacteria produce some vitamins. Large intestinal vitamin K is very important in chickens, for instance. Bacteria also produce gases, the most important of which are carbon dioxide and methane.

Monogastric herbivores like the horse, rabbit, guinea pig, and elephant have an extensive colon and functional cecum. Carnivores, by contrast, have a very short large intestine with nonfunctional ceca. The combined colon and cecum of the monogastric herbivores is comparable in size to the rumen of ruminants and has a large fermentation capacity. The large intestines and ceca in monogastric herbivores function much as the rumen does but with less advantage to the animal. The reason is twofold. Much of the good nutrient content has already been removed from the feed by the digestion and absorption of the digestive tract prior to the feed reaching the cecum. Thus, the cecum has lower quality feed to work with than does the rumen. The second reason is that absorption is less from the cecum than the rumen. Very significant digestion does take place, however. Microorganisms break down cellulose in the cecum and large intestine, much as in the rumen. B-complex vitamins are produced. VFAs are produced, absorbed, and used in all monogastric herbivores as an energy source, similar to what happens in the ruminant. A large amount of bacterial protein is also manufactured in the cecum. However, animals must employ behavioral adaptation to be able to use this protein because there are no digestive secretions into the large intestine by the animal. The large intestine can only absorb free amino acids, not whole proteins, so the microbial protein remains unused. The adaptive mechanism is called **cecotrophy,** which is a form of pseudorumination. Animals who practice cecotrophy eat the contents of their cecum and digest it after it has been fermented in the cecum. Rabbits, for example, practice cecotrophy. They have two types of feces. One is the pellet type, which is what people usually see. The other is a soft feces that the rabbit eats. This soft feces is material that has been fermented in the cecum. The bacterial protein produced by the fermentation is digested the second time around by the upper gut. If a rabbit is denied the option of practicing cecotrophy and is on a poor diet, it will die of malnutrition because it will be deficient in protein and B vitamins. Cecal fermenters who do not practice cecotrophy, such as horses, depend more on dietary protein and B vitamins than do rabbits or ruminants. Thus, they need more dietary proteins and B vitamins in their diet.

Cecotrophy The process by which mucus-covered soft fecal pellets are expelled from the intestine and consumed by the animal.

The omnivore large intestine is generally less capable than that of the herbivore, but more capable than that of the carnivore. Vitamin synthesis and water and electrolyte absorption are similar to that of the carnivores. Cellulose digestion in these animals is a function of retention time. The longer it is retained, the more likely some digestion will take place. Studies indicate that up to 18–20% crude fiber digestion in high-fiber diets fed to swine is possible. The usefulness of this is unclear, however, because the role of volatile fatty acid absorption and utilization in the pig is poorly understood. Because swine in modern swine production facilities are rarely fed much fibrous feed, the argument is moot.

Defecation is the discharge of excrement from the body via the rectum or cloaca. Internal and external anal sphincters control the exit of material from the body. Defecation is initiated by the defecation reflex, which is stimulated by the pressure of feces in the rectum. This reflex is assisted by parasympathetic nervous signals that intensify the peristaltic waves of the large intestines. Many animals also use the Valsalva maneuver. They breathe deeply, close the glottis, and then flex the abdominal muscles. This puts pressure on the fecal contents and helps expel them.

Defecation The act of expelling fecal matter from the large intestine via the rectum or cloaca.

The contents of the fecal material include undigested feed, residues of digestive enzymes, sloughed cells, and bacteria. The quantity of feces is affected by how well the feed is digested. Feeds low in digestibility contribute more undigested material to the feces. In addition, the poorly digested material causes an increase in the amount of sloughed cells from the wall of the intestine.

Micturition is urination. The components of urine include the nitrogen compounds—urea in mammals and uric acid in birds and other species. Uric acid requires much less water from the body to excrete. Also included are minerals and water. The kidney is a major regulatory mechanism for keeping the body appropriately hydrated and for removing various wastes from the body.

Micturition The act of urinating.

DIGESTION IN THE PIG

The pig is omnivorous and monogastric (Figure 6–3). A pig's mouth is used primarily for grinding feed by the teeth and mixing with saliva. The saliva, which has a pH of about 7.4, moistens feed and helps in the chewing and swallowing process. The

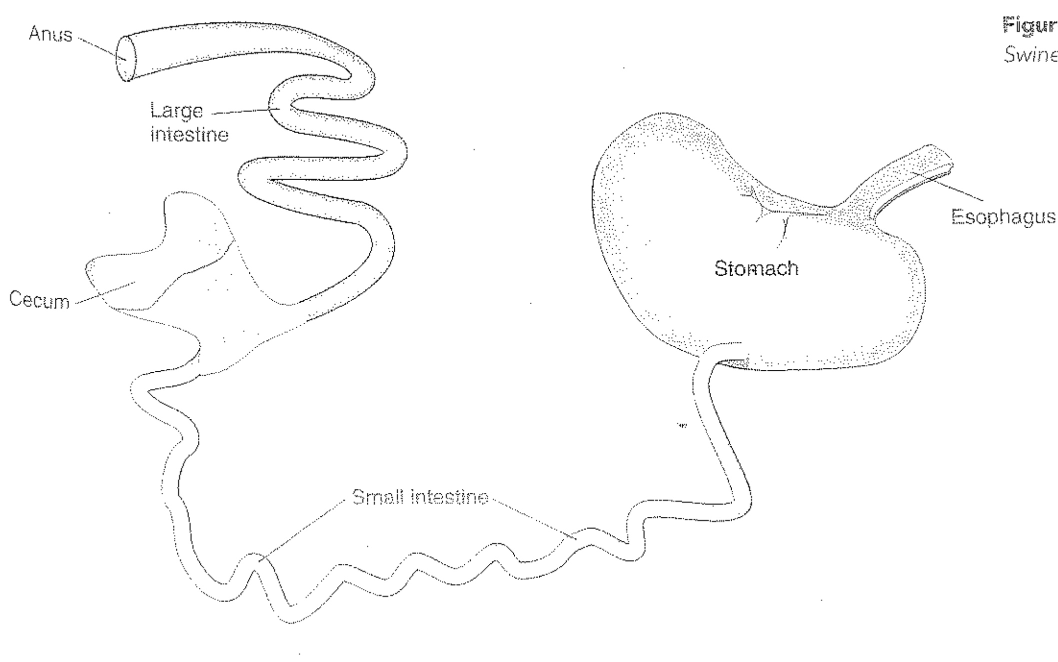


Figure 6–3
Swine digestive tract.

pig is the only farm mammal in which any amount of the enzyme salivary amylase is secreted in the saliva. The salivary amylase is relatively weak compared to that in human saliva, which is about 100 times more powerful. Amylase begins to break down the starch in the feed. However, this is of very little nutritional importance because the feed does not stay in the mouth long enough for starch breakdown. The pH is too low (acidic) in the stomach for amylase to act on the starches. The stomach of the full-grown pig has a capacity of about 2 gals.

The enzymes contained in the gastric juices of the pig are those expected in a monogastric animal. One exception is that rennin, the enzyme that coagulates milk, is not found in the pig's gastric juice. Digestion of protein is completed in the intestine and most fat digestion occurs in the small intestine. The pig requires about 24 hours to empty a full stomach.

The small intestine of the full-grown pig is about 60 ft long, has a capacity of about 2.5 gals, and is divided into three sections. The function of the small intestine is to continue the process of digestion by means of the pancreatic juice, bile, intestinal juice, and movements of the intestinal wall. A large amount of absorption of nutrients also occurs in the small intestine of the pig.

Pancreatic juice contains a number of enzymes that aid in the digestion of proteins, fats, and carbohydrates, as well as sodium carbonate and sodium bicarbonate, which neutralize acid from the stomach. The pancreas also produces insulin, which plays an important role in carbohydrate metabolism. Trypsin is initially secreted as trypsinogen and activated by calcium ions and the enzyme enterokinase, which is found in the intestine. Trypsin breaks down protein into amino acids and peptides. Chymotrypsin is secreted as chymotrypsinogen and activated by the action of trypsin in the intestine. It converts proteins into peptides and amino acids and has a coagulating action on milk. Carboxypeptidase acts on peptides and breaks them down to amino acids. All three of these enzymes continue the protein digestion that was started by pepsin in the gastric juice, and attack undigested proteins. Pancreatic lipase (steapsin) converts fats into fatty acids and glycerol. This action is most effective after the bile has emulsified the fats. Pancreatic amylase (amylopsin or pancreatic diastase) converts starch to maltose. Maltase changes maltose into glucose. Sucrase (invertase) changes sucrose to glucose and fructose. Lecithinase hydrolyzes the phospholipid lecithin.

Bile assists in digestion and absorption of fats and aids in absorption of fat-soluble vitamins. Bile may also activate pancreatic lipase and accelerate the action of pancreatic amylase.

The large intestine in the adult pig is about 16 ft long, has a capacity of 2.5 gals, and consists of the cecum and the colon, which terminates as the rectum and anus. In the mature pig, the cecum is about 9.5 in. in length, with a capacity of about 0.5 gals. The colon in the mature pig is about 16 ft long and has a capacity of 2.0 gals. The primary functions of the large intestine are to absorb water and to act as a reservoir for the waste materials that constitute the feces.

DIGESTION IN THE RUMINANT

The most important difference between ruminants and nonruminants is the complex stomach of the ruminants and the very different digestion that takes place there. Because ruminants represent the largest percentage of the domestic herbivores, we discuss them in detail. The main function of the complex stomach of the ruminant is to allow the animal to use roughage (cellulose) as a source of energy. Microbial populations housed by the ruminant in the first three compartments ferment feed. The end products of the fermentation provide nutrients to the animal that would otherwise be unavailable for any productive use.

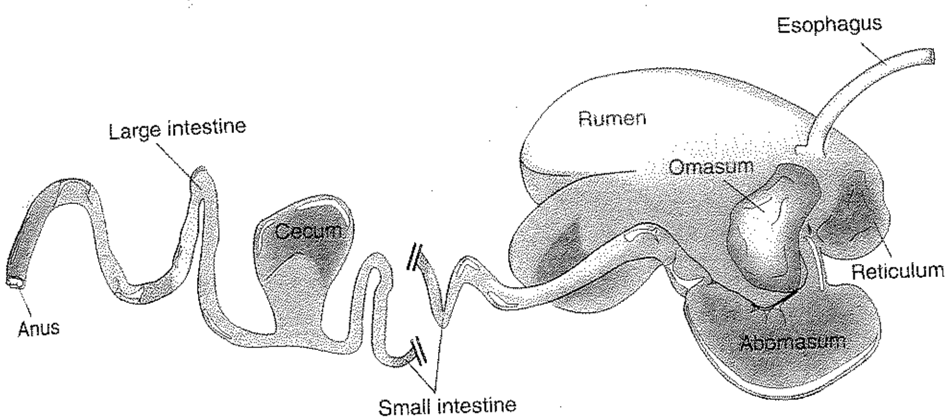


Figure 6–4 *Digestive system of the ruminant.* (Source: Modeled on Jurgens, 1993, p. 44.)

Rumen The largest of the ruminant forestomachs. Contains microorganisms that degrade complex carbohydrates and produce volatile fatty acids, amino acids, and vitamins to the host animal.

A ruminant typically fills the **rumen** rapidly, taking little or no time to chew its meal, and then finds a place to rest and chew. During rumination, the animal regurgitates the food eaten earlier and spends time chewing it. The particle size of the feed is broken down mechanically in this way and its surface area is increased manyfold. This increased surface area allows the microorganisms many more places of access than would otherwise be available. When one mouthful is sufficiently chewed, it is re-swallowed, another is regurgitated, and the process is repeated. A ruminant may spend a third of its life in this process. The more fiber in a diet, the more the animal will ruminate, and vice versa. Straw stays in the rumen much longer than feed of higher quality like corn silage, because of the need to ruminate and thereby help the microorganisms.

Anatomy of a typical ruminant stomach is shown in Figure 6–4. The complex stomach is comprised of four compartments: rumen, reticulum, omasum, and abomasum. Common names for these compartments are *paunch* for the rumen, *honeycomb* and *hardware stomach* for the reticulum, *manyplies* and *Stockman's Bible* for the omasum, and *true stomach* for the abomasum. The rumen and reticulum are often called the *rumino-reticulum* or *reticulo-rumen complex* because material passes freely between them and no wall separates them.

The contents of the rumen generally equal about 20% of the body weight of the adult animal. The combined capacity of the rumen, reticulum, and omasum is approximately 50 gals in an adult dairy cow, which provides significant fermentation capacity. The relative volume of the rumen is 80%, the reticulum 5%, the omasum 7–8%, and the abomasum 8–9%. The relative amount of dry versus wet material in the rumen is variable depending on what the animal has consumed and what has been absorbed. This can range from 5–60 gals of liquid and from 5–50 lbs of solid.

Forestomachs The name given to the three digestive compartments of the ruminant tract that are placed anatomically before the true stomach.

The rumen, reticulum, and omasum are collectively known as the **forestomachs.** The lining of these organs is nonglandular and does not produce mucus or enzymes. The abomasum, or true stomach, is lined with a true mucous membrane, and gastric juice is secreted, as in the stomachs of all mammals. Generally speaking, from the abomasum to the anus, the ruminant tract is much the same as a monogastric tract.

The reticular groove contracts and forms a tube that acts as a bypass of the rumen and empties into the omasum (Figure 6–5). This groove functions to keep milk out of the young ruminant's undeveloped rumen. If a calf drinks milk too quickly or if the groove does not close, milk can get into the rumen of the calf. The milk can't be adequately digested in the immature rumen and rots. The calf develops a severe case of diarrhea (scours) owing to the proliferation of bacteria and production of toxins in the rumen.

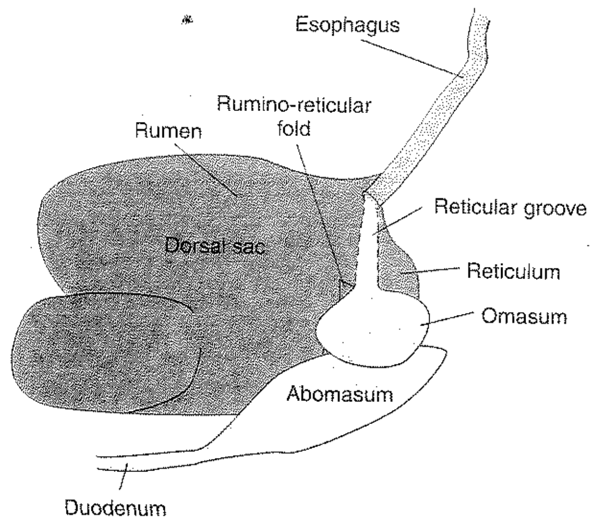


Figure 6–5
Side view (right side) of the rumen.

The main function of the rumen is to act as a site of anaerobic bacterial fermentation. Undeveloped at birth, it begins developing in response to the young animal's eating solid food and can have some fermentation as early as 6–8 weeks of age. All of the food consumed by the ruminant animal enters the reticulorumen. Some passes through quickly and isn't affected, but 85–95% is fermented to some degree. The bacteria in the rumen digest carbohydrates (cellulose, starch, and so on) and other plant materials and produce volatile fatty acids (VFAs) as an excretory by-product. VFAs are absorbed by the animal across the rumen wall and supply about 50% or more (maybe up to 70% in some cases) of the energy requirement for the ruminant. The rumen wall is covered with small fingerlike projections called **papillae.** Papillae function to increase the absorptive surface of the rumen.

Papillae Small fingerlike projections that greatly increase the surface area of the small intestine.

A major benefit of microbial fermentation is the protein manufactured by the microorganisms as they live and reproduce. Bacteria can even convert nonprotein nitrogen (NPN) such as urea into bacterial protein, which the animal subsequently uses. The bacteria pass out of the rumen and down the tract with the feed and are digested in the abomasum and small intestine. The amino acids released by the action of the animal's enzymatic digestion often meet the protein requirements of the animal. The microorganisms are about 50% crude protein with 3% lysine content. Their quality is similar to that of soybean meal, which is an excellent quality feedstuff. The bacteria also contain energy, vitamin K, and water-soluble vitamins that the animal is able to digest, absorb, and use. The formation of these vitamins by the rumen bacteria frees the ruminant from dietary water-soluble requirements under normal circumstances. The microorganisms do not synthesize vitamins A, D, and E. The bacteria also produce enough essential fatty acids for the animal.

Another important function of the rumen is to store food. This is probably how ruminants evolved—they would eat rapidly, run and hide in the woods, and chew their meal. This helped them avoid predators by minimizing their time in the open grasslands where they were vulnerable to predators.

The reticulum functions as a site of microbial action, just the same as the rumen. The reticulum also acts as a pacemaker of rumen contractions. The contractions start with the reticulum and spread to the rumen. These rumen contractions are very strong and caused by contraction of the powerful rumen muscles. They function to mix the rumen contents and are essential for optimum microbial digestion. These contractions also serve to move the contents through the digestive tract. The heavier particles settle in the reticulum and are passed on through the omasum to the abomasum. The lighter particles float on the top of the rumen; these particles are then regurgitated and subjected to remastication.

The omasum absorbs water, electrolytes, and VFAs and reduces particle size of feed before it enters the abomasum.

The abomasum of the ruminant is equivalent to the true glandular stomach in monogastrics and has the same functions. Folds in the wall of the ruminant abomasum provide extra capacity and help the ruminant handle the large volume of dietary fiber.

Eructation is a very important mechanism for ruminants. The large quantities of gas produced by the rumen microorganisms as a by-product during fermentation (up to 600 L/day in a dairy cow) must be removed. Contractions of the upper sacs of the rumen force the gas toward the esophagus, which dilates, and the gas escapes. Much of the gas goes into the trachea and lungs. This provides a muffling effect and reduces the noise level considerably from what it would otherwise be. This too probably developed as a defense mechanism. It did little good for the herd to hide in the woods if a chorus of belching noises attracted every predator within hearing distance.

Eructation Belching. Removing gas from the rumen via the esophagus.

The Fermentation Process

Rumen microorganisms and the ruminant animal live in **symbiosis.** The animal benefits because the microorganisms digest feeds it could not otherwise use and generate nutrients it needs. This makes feeding the ruminant more complicated because feeding the ruminant actually involves feeding the microorganisms as well as feeding the animals. The ruminal environment is maintained by the animal to support the microorganisms, which are thus provided with a near ideal set of living conditions. These include warmth, moisture, a food supply, removal of the end products of digestion, darkness, and an **anaerobic** environment. In addition, ruminal contractions keep the contents mixed, and rumination reduces the particle size of the feed for easy access by the microorganisms.

Symbiosis A relationship where dissimilar organisms live together or in close association.

Anaerobic Conditions that lack molecular oxygen.

Many different bacteria are found in the rumen and include populations that specialize in digesting cellulose, hemicellulose, starch, proteins, sugars, acids, and producers of ammonia, vitamins, and methane. Concentrations can range from 15–50 billion/mL of rumen fluid.

Nearly 40 species of ciliate protozoa also occupy the rumen. Typically, any individual animal has only a dozen or so different species. Many factors affect the concentrations of protozoa, which can number up to a million per milliliter of rumen fluid. Protozoa use the same substrates as the bacteria and dine on bacteria as well. Some believe they help prevent bacterial overgrowth. Protozoa are closely associated with the food particles and tend to stay in the rumen rather than passing on down the tract for digestion.

Virtually everything the ruminant consumes is affected by the rumen fermentation. Some feeds are changed tremendously; others less so. Both simple and complex carbohydrates are fermented in the rumen. VFAs are a major product of ruminal fermentation. The VFAs commonly produced in the rumen are acetate, propionate, butyrate, isobutyrate, valerate, and isovalerate. The VFAs are very important. As an energy source, they may provide as much as 50–70% of the total energy needs of the animal. Bacterial cells provide 5–10% of the energy to the animal, and feed that is digested enzymatically amounts to 20–30% (Figure 6–6).

Much of the protein is broken down by microorganisms to ammonia and organic acids. The microorganisms then use the ammonia to manufacture amino acids for their own use. NPN sources can also be used by the microorganisms.

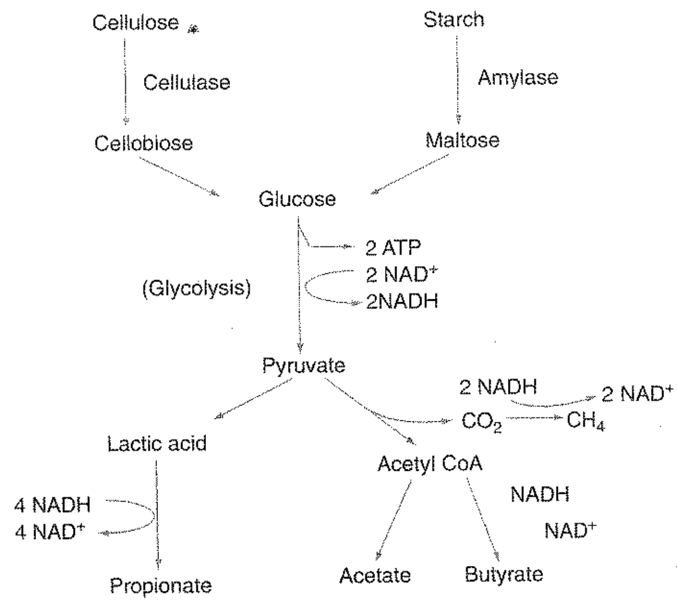


Figure 6–6
VFA synthesis in the rumen by microorganisms.

This allows us to feed urea and other NPN sources to ruminants as a means of reducing costs. Most plant sources are low in lipids, and those found in feeds aren't changed much by the fermentation process. High levels of fat are bad for the microbes and reduce the overall ability of the microorganisms to do their job.

Gas is a major product of fermentation and may amount to up to 600 L/day, as we mentioned earlier. Heat is also a major product of fermentation. The heat of fermentation is a part of the total heat increment of the animal, which is useful in winter to keep the body warm but can be detrimental in hot weather.

Advantages and Disadvantages of the Ruminant System

There are both advantages and disadvantages to the ruminant digestive system when compared to that of the nonruminant animal. Microbial fermentation has the potential to digest feedstuffs that the animal's enzymatic digestion processes cannot. This increases the feeding value of such feeds as prairie hay, corncobs, and wheat straw. Essential nutrients not found in the animal's diet such as vitamins, amino acids, and fatty acids are manufactured by the microbes and absorbed and used by the animal. If microbial fermentation occurred only in the cecum, most of these nutrients would be excreted in the feces.

A disadvantage is that the fermentation processes in the reticulo-rumen have the potential to decrease the overall quality of the ruminant animal's diet by destroying essential nutrients such as vitamins, amino acids, and fatty acids that are found in the feed. Much current interest has been expressed in bypassing high-quality feedstuffs such as soybean meal and starch and not allowing the microbes to digest them. The fermentation process also requires and wastes a considerable quantity of energy. A significant portion of the dietary energy is lost as heat and gaseous products of incomplete bacterial metabolism. This explains in part why the feed consumption required to result in 1 lb of body weight gain is about 6–8 lbs for a growing steer compared with about 3 lbs for a growing pig. Fortunately, we do not have to feed ruminant animals high-quality feeds throughout their production cycle. The ruminant animal provides us with an ideal mechanism to convert low-quality feeds not fit for human consumption into high-quality food products. Greater susceptibility to digestive upsets such as bloat (the accumulation of massive quantities of gas in the rumen) and acidosis (reduced rumen pH), which damages the rumen wall and leads to lowered productivity and liver abscesses, are other disadvantages.

DIGESTION IN THE AVIAN

The digestive organs of fowl (Figure 6–7) are similar to those of other monogastrics except for the lack of teeth and the presence of the gizzard and the crop. The mouth is not sharply separated from the pharynx. Most birds have no soft palate or teeth, and only small numbers of poorly developed salivary glands. Salivary amylase exists in the saliva but is of little value. There is no digestion in the mouth. The esophagus in the avian tract is modified. The crop is a dilation of the esophagus that is present in most species, but not all. It functions as a food storage organ and as a moistening reservoir. The size of the crop varies with the eating habits of the bird and between species. In doves and pigeons, the crop produces "pigeon milk" or "crop milk," which is used to feed the young. Fermentation occurs in the crop in some species.

The proventriculus is equivalent to the glandular stomach in mammals or the abomasum in ruminants. It is small in some species, such as chickens or pigeons. It is large in some fish-eating species (i.e., those consuming high-protein diets). The proventriculus is the site of gastric juice production (HCl and pepsin) and has a pH of 4. Ingesta passes through in a matter of seconds, so virtually no digestion takes place. Carnivorous birds are an exception—there is digestion in their proventriculus.

The gizzard, or ventriculus, is a highly specialized grinding organ. It is very muscular but varies in muscularity depending on the type of food consumed. It may

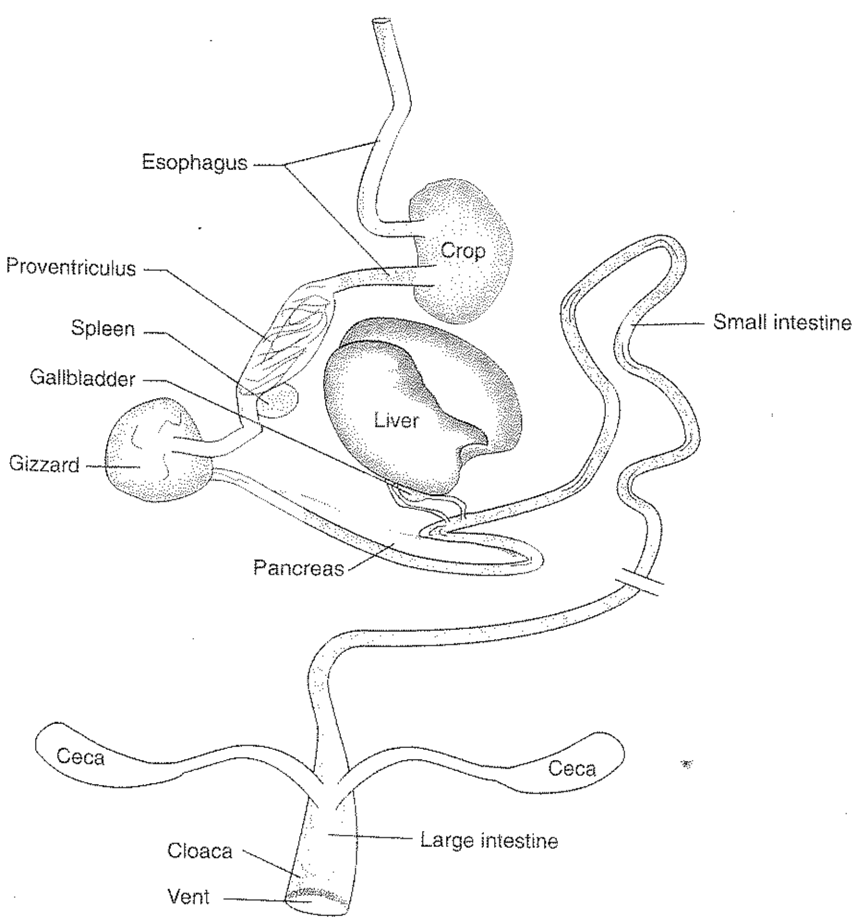


Figure 6–7
Digestive system of the avian.

be large and well developed in wild animals and smaller and less developed in commercially raised species that eat preground rations. In free-ranging birds, the gizzard contains grit to aid in the grinding of feed to smaller particles; however, with modern preground rations, grit is unnecessary. No enzymes are secreted; however, the enzymes from the proventriculus work here.

The small intestine functions in digestion and absorption of feed and nutrients just as in other monogastrics. The first part of the small intestine is the duodenum just as in other animals, but there is no specifically separated jejunum or ileum like that of mammals. The length of the duodenum varies among and between species, especially with eating habits. It is longer in herbivorous than in carnivorous birds. Generally the same enzymes found in mammalian species are present except for lactase. Milk by-products are rarely fed to chickens for this reason.

The ceca are located at the junction of the small and large intestine. There are two ceca in the avian. The size is influenced by the type of diet—the ceca are larger when the animal consumes high fiber. They open into the large intestine via the muscular ileocecal valves. Water reabsorption occurs in the ceca along with some fiber digestion; perhaps as much as 18% of total fiber and water-soluble vitamin synthesis occurs in the ceca by bacteria. The modern chicken is fed little fiber and therefore does not make use of its ceca.

The large intestine is relatively short in birds, only 2–4 in. It is not divided into a distinct rectum or colon as it is in mammals. From a digestive perspective, the large intestine is more important in water absorption than in any other function. However, vitamin K synthesis and absorption do occur here in the chicken. The cloaca is the common orifice for waste elimination (feces and urine), copulation, and egg laying in females.

DIGESTION IN THE HORSE

Figure 6–8 illustrates the horse digestive system. The horse is a nonruminant herbivore. Horses, rabbits, and guinea pigs are all capable of using roughage because they have an active cecal bacterial population that digests fiber. In this section, we explore the digestion of the horse as a model for the cecal fermenters.

The horse accomplishes prehension with its teeth, a flexible upper lip, and tongue. The horse has both vertical and lateral jaw movements. In addition, the upper jaw is wider than the lower jaw. Because of this, horses chew on only one side of

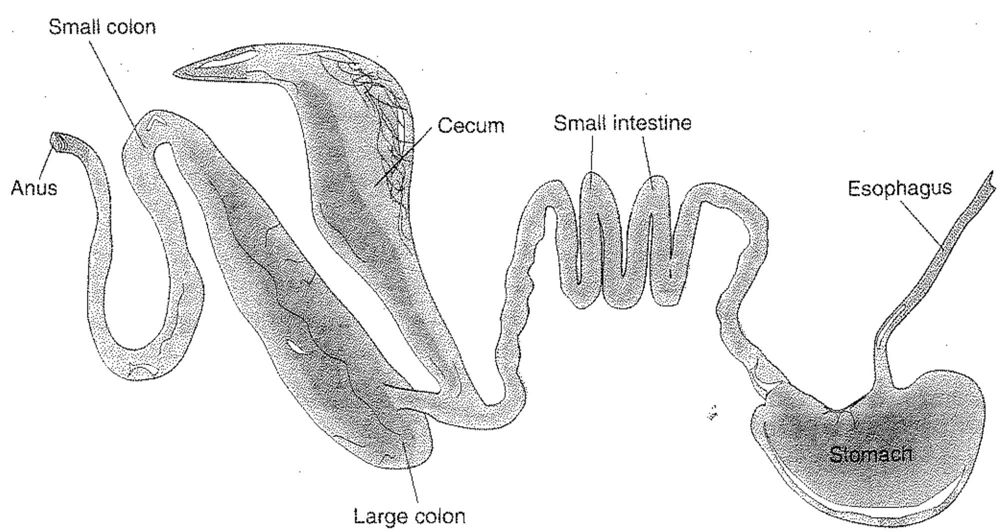


Figure 6–8
Digestive system of the horse.

the mouth at a time. The saliva of the horse contains no enzymes but is important as a lubricant for the coarse material the horse eats. Total secretion is copious. A mature horse may secrete up to 10 gals per day if it is consuming hay or other similar material. The esophagus of the horse has only one-way peristaltic movements, which makes it almost impossible for the horse to regurgitate.

The stomach of the horse has some important distinctions compared to the stomachs of other mammals. Perhaps the most distinctive is that the stomach capacity is smaller. A pig less than half the size of a horse can have a stomach as large. A cow of equal size has an abomasum that is 50% larger. The horse's stomach provides only 8% of the capacity of the tract, or approximately 3–4 gals of capacity. The horse stomach is also unique in that it does not have equivalent muscular activity to that of other species. The feed tends to arrange itself in layers because of this lesser activity. These two factors result in the horse being more susceptible to stomach disorders than are other species. **Colic** and ruptured stomachs both occur, with colic very common. Horses should be fed small portions several times daily if possible. At a minimum, twice-a-day feeding is desirable with sufficient hay to help avoid stomach disorders.

Colic A broad term that means digestive disturbance, especially in horses.

The small intestine of the horse is similar to that of other monogastrics except for the absence of a gallbladder. The horse evolved as a continual eater and had no need for storage of bile to help with digestion of food consumed in meals. Instead, bile is secreted directly and fairly continually into the duodenum at a rate of approximately 300 mL/hr.

The large intestine of the horse is divided into the cecum, large colon, small colon, and rectum and is 25 ft long in an average-sized horse. It accounts for over 60% of the total gut capacity and is equal to about three-fifths the size of the large intestine capacity in a comparably sized ruminant. The cecum and large colon contain a bacterial population similar to that of the rumino-reticulum of ruminants in both numbers and kinds of microorganisms. Bacterial fermentation produces VFAs similar to those of the ruminant, which are absorbed and used by the animal. The horse on a forage diet receives the majority of its energy in the form of these VFAs from the large intestine. These bacteria also synthesize water-soluble vitamins that are absorbed from the large intestine, but in limited amounts. Bacterial synthesis of protein occurs, but the horse is not able to absorb this product because of the lack of enzymes and absorptive mechanisms. Because this protein is not subject to action of the digestive juices, the horse benefits little from it unless it practices **coprophagy.** Sometimes, horses on a poor diet practice coprophagy in an attempt to balance their nutrient needs. The cecum is the primary area of water reabsorption from intestinal contents, although additional amounts are absorbed from the colon.

Coprophagy The act of eating feces.

The soluble carbohydrates are digested and absorbed in the small intestine much as in any monogastric. The fiber fractions are fermented in the large intestine and colon. The products are essentially the same as those of a rumen fermentation. The VFAs are even produced in almost identical molar concentrations as those in the rumen. The VFAs are absorbed from the large intestine and used as an energy source by the cells of the horse. The horse is only about two-thirds as effective at fiber digestion as the ruminant. This is generally believed to be because feed has a much more rapid rate of passage through the horse than the ruminant. The fats found in a horse's ration are digested and absorbed in the small intestine.

The absence of a gallbladder does not seem to cause the horse any problem. Fats in rations of up to 20% fat are digested 90% or better. Proteins are digested in the horse similarly to other monogastrics and must receive the essential amino acids in the diet. Horses should receive better feed than cattle receive if we expect them to perform to their potential.

SUMMARY AND CONCLUSION

Different species have very different digestive tracts. These differences are both anatomical and functional and in many ways dictate how animals must be fed. However, for all their differences, there are also tremendous similarities. The overall goal of digestion is the same for all species: to release nutrients for the animal to absorb and metabolize in order to maintain and produce.

STUDY QUESTIONS

1. Define digestion.
2. What are the three major methods of digestion? Describe them.
3. Why do different animals use very different kinds of feeds?
4. What are the stomach types in livestock?
5. Define carnivore, omnivore, and herbivore.
6. What is prehension?
7. Define mastication. How do different animals accomplish this?
8. What is salivation? How do mastication and salivation help the animal?
9. What do you think dictates the amount of saliva that various species produce?
10. What are the components and functions of saliva?
11. Define deglutition.
12. What is the role of the stomach in digestion?
13. What are the three portions of the small intestine, and what is the function of each?
14. What does bile do? Where does it come from?
15. What does pancreatic juice do? Include a description of the function of each enzyme found in pancreatic juice.
16. What is the function of the large intestine? What do bacteria do in the gut of a monogastric herbivore?
17. Why do rabbits practice cecotrophy?
18. Describe how an animal defecates.
19. What are the components of urine?
20. Describe how a bite of feed is digested by the pig from prehension to defecation.
21. What is the major anatomical difference in ruminants and nonruminants?
22. Describe the anatomy of the ruminant tract. What are the common names of the four ruminant digestive compartments found between the esophagus and the small intestine?
23. What is the relative volume of each compartment in the ruminant "stomach"?
24. What is the reticular groove and what does it do?
25. What is the function of the rumen?
26. Why are VFAs of importance to the ruminant, and what does the animal do with them?
27. What is the relative quality of the protein manufactured in the rumen?
28. Name the nutrients produced by rumen fermentation.
29. What is the function of the reticulum? The omasum? The abomasum?
30. Describe eructation and discuss the consequences if a ruminant is unable to eructate.
31. Describe symbiosis. How do ruminants and their microbes qualify for status as symbiotic partners?
32. What kinds of microorganisms are found in the rumen?
33. What is the relative importance of VFAs to the energy contribution of a ruminant animal?
34. What is the composition of the gas coming off a ruminant fermentation?
35. State clearly the advantages of the ruminant digestive system.
36. Why don't ruminants practice cecotrophy?
37. What are the disadvantages of the ruminant digestive system?
38. Why is the feed conversion ratio for ruminants so much poorer than it is for monogastrics?
39. What are the major anatomical differences in the avian and the pig? Describe each along with its function.
40. How does digestion occur in the avian? What are the differences in the digestive processes of a chicken and of a pig?
41. Describe the significance to the horse of being a cecal fermenter.
42. How much saliva does the horse produce?
43. What are the unique features of a horse's stomach?
44. Describe in detail what happens in the large intestine and cecum of the horse.
45. Why must we feed essential amino acids to horses but not to cows?

24. contracts and forms a tube that acts as a bypass of the rumen and empties into the omasum

29. Reticulum - microbial action
omasum - absorbs water, electrolytes, and VFA's and reduces particular s
abomasum - same as monogastric stomach. Break down nutrients