THE DIGESTIVE PROCESSES IN DOMESTIC ANIMALS

by H. W. Schoening

THE processes by which different food materials from the outside world are taken into the animal body and made ready for use are complex and wonderful. This article tells the story of digestion in cattle, sheep, pigs, horses, dogs, cats, and fowl in as much detail as is possible in a short space. It gives a background for the articles that follow on the nutritional requirements of animals and feeding practices.

Nearly all food materials are in too complex and insoluble forms as they are consumed by either animals or man to be absorbed and assimilated. The specific purpose of digestion, therefore, is to convert these food substances into simple and soluble materials fit for absorption and assimilation. All animals except the most primitive types are provided with several highly specialized digestive organs.

The digestive tract may be described as a tube extending from the lips to the anus, constructed with such dilations and constrictions throughout its length as to form a number of compartments, each of which has a specific function in the digestive process. The contents of the tube, that is, the foods taken in, or ingested, by the animal, are propelled by wavelike movements known as peristalsis. In addition to moving the food along the tract until it is eventually expelled, the movements serve to mix the food with the digestive juices, to promote absorption of digested material, and to enhance the flow of blood and lymph through the intestinal vessels.

The degree to which this system has been elaborated in the several species under consideration suggests the kind and character of food usually eaten. The kind of foods habitually used brings each species of animal under one of three classifications: Carnivorous (meat-eating), herbivorous (plant-eating), or omnivorous (eating both meat and plant substances). Of the herbivorous species, the horse, ox, and sheep are the most important among domesticated animals; the dog and cat exemplify the carnivorous; and the pig and the barnyard fowl are representative of the omnivorous type.

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It is quite obvious that the herbivorous animal needs a different kind of digestive apparatus from that of the carnivorous animal, while the omnivorous one naturally needs a set of digestive organs adaptable in some degree to either type of diet. These differences involve the method of acquiring food as well as of preparing it for digestion and of actually digesting it.

If the finding and selection of food are considered as essential preliminaries to the digestive process, it would seem proper to enumerate the senses of sight, smell, touch, and, in the case of predatory animals, hearing also as preparatory functions preceding the intake of food. The powers of sight and scent are useful to all animals in finding their food. In the case of the horse, the sensitive nerve structures of the upper lip assist the animal to discern by the sense of touch the presence of edible food substances.

Strictly speaking, however, the digestive process begins with the prehension, or taking up of food; continues with its mastication (chewing), insalivation (mixing with the salivary secretions), deglutition (swallowing), and the digestion, absorption, and assimilation of those food elements that are of nutritive value; and terminates with defecation, or the excretion of the remaining ingested matter not capable of being absorbed or utilized as nourishment. To perform these functions, the digestive tract of the animal is equipped with mouth, teeth, tongue, pharynx, esophagus, stomach, intestine, and anus. Even among the various common domestic species, differences exist in certain portions of the digestive tract to accommodate the special requirements of the species.

**TAKING OF FOOD**

Prehension, or the taking up of food, is accomplished in most animals by means of the lips, teeth, and tongue. In the horse, prehension is performed by the strong and flexible upper lip and incisor teeth (fig. 1). When grazing, this animal employs lips and incisor teeth, cutting or tearing the vegetation seized by jerking movements of the head or neck. The ox is not endowed with such mobile lips or with upper incisor teeth (fig. 2). Instead it uses its long, muscular tongue to pull the grass or hay into its mouth, cutting it off between the lower incisors and the upper gum by an upward movement of the head and neck. The sheep seizes its food in much the same manner, but it makes use of its mobile lips rather than its tongue in gathering food into the mouth. The native habit of the pig of burrowing or rooting to find its food has survived the domestication of this species. Prehension, however, is accomplished by the movements of the pointed lower lip and is assisted by the teeth and tongue (fig. 3). In the dog (fig. 4) and the cat, the food is seized by the incisor and canine teeth and brought into the mouth by jerking movements of the head and jaws. The organ of prehension in fowls is the beak. The fowl picks up its food in its toothless beak and passes it to the base of the tongue preparatory to swallowing.

Drinking is accomplished by the horse, ox, sheep, and pig by sucking the fluid into the mouth by the aid of the tongue and pharynx. The lips form a small opening which is dipped beneath the surface of the water, and the tongue moving back and forth like a piston in a cylinder
creates a negative pressure in the mouth which causes water to pass into the mouth with the backward thrust of the tongue and to be swallowed with the forward thrust. The pharynx serves as a valve in this pumping process. The dog and the cat take up liquids by lapping with the tongue. In the fowl, drinking consists merely of

**Figure 1.**—The mature horse has 6 incisors in upper and lower jaw and 6 molars on each side, upper and lower. The male horse has 2 canines in upper and lower jaw. The mare has no canines. Total for horse, 40 teeth; total for mare, 36 teeth. (After F. Smith, A Manual of Veterinary Physiology.) Capacity of stomach, 4.75 gallons; of small intestine, 16.86 gallons; of cecum, 8.8 gallons; of large intestine, 25.36 gallons. The small intestine is about 73.6 feet long. The cecum is 40 inches long. The large intestine is approximately 21.22 feet long. (Intestinal proportions after H. H. Dukes, The Physiology of Domestic Animals.)

**Figure 2.**—The ox has 8 incisors in the lower jaw and no upper incisors. This species has 6 molars on each side in the lower and upper jaws. It has no canines. Total, 32 teeth. (Smith.) Capacity of stomach, 66.71 gallons; of small intestine, 17.43 gallons; of cecum, 2.6 gallons; of large intestine, 7.4 gallons. Length of small intestine, 150.38 feet; of cecum, 2.89 feet; of large intestine, 33.3 feet. (Dukes.)
scooping up the fluid into the lower beak and then elevating the head
to permit it to flow by gravitation into the crop or stomach. The
pigeon's method of drinking, however, more nearly resembles that of
the horse or ox than that of other birds. This bird thrusts its beak
deep into the water and by a very rapid movement of the tongue
sucks in the liquid.

Figure 3.—The pig has 6 incisors, upper and lower; 2 canines, upper and lower; 7
molars on each side, upper and lower. Total, 44 teeth. (Smith.) Capacity of stomach,
2.11 gallons; of small intestine, 2.43 gallons; of cecum, 0.31 gallon; of large intestine,
2.3 gallons. Length of small intestine, 60 feet; of cecum, 9.05 inches; of large intestine,
16.4 feet. (Dukes.)

Figure 4.—The dog has 6 incisors, upper and lower; 2 canines, upper and lower; 6 molars
in each side of the upper jaw, 7 molars in each side of the lower jaw. Total, 42 teeth.
(Smith.) Capacity of stomach, 1.14 gallons; of small intestine, 1.7 quarts; of cecum
1.5 fluid ounces; of large intestine, 15.36 fluid ounces. Length of small intestine, 13.67
feet; of cecum, 3.12 inches; of large intestine, 1.97 feet. (Dukes.) (The figures for
size and capacity of the internal organs are average; they would of course vary with
the size of the animal.)
CHEWING

After the prehension of food, the next step, except of course in the toothless fowl, is mastication. Mastication, or chewing, of food is accomplished by means of grinding teeth so situated in the upper and lower jaws that they can be employed to crush and divide the food substance preparatory to swallowing. The mechanism of mastication involves the use of the two jaws, the tongue, and the cheeks. The upper jaw is a rigid portion of the head, while the lower jaw is hinged to the skull so that it can be moved in a vertical and to some extent in a lateral or diagonal plane against the upper jaw. These movements are brought about by the muscles of the jaws. There is a pronounced sidewise or lateral movement of the lower jaw in the ruminants (ox and sheep), slightly less in the horse, and still less in the omnivorous pig. In the carnivores (dog and cat), there is very little lateral movement.

Striking differences exist in the chewing structures of the various species, particularly as to the kind of teeth and their functions. Some animals have three kinds of teeth and others two kinds. The front or incisor teeth, which occur in all mammals, are used for detaching or cutting the food into suitable proportions for chewing. These teeth are in both the upper and lower jaws except in ruminants, in which the upper incisors are lacking. Ruminants, however, have a tough upper gum known as a dental pad, against which the lower incisors compress the forage in cutting or tearing it off. The canine teeth or tusks function both for seizing food and for combative purposes.

The masticatory teeth, or molars, which are common to all species, are located laterally in both upper and lower jaws. Food material brought between the opposing rows of teeth by the movements of the cheeks and tongue are comminuted, or reduced to fine particles, by the crushing or grinding movements of upper and lower molars as they are brought together during the chewing process. In the horse, ox, and sheep, the grinding surface of the molars slopes sidewise, those of the upper jaw presenting an acute angle on the outer side and those of the lower jaw being pointed on the inner side. In the pig, dog, and cat, the grinding surface is more nearly at right angles to the long axis of the tooth.

Mastication in the horse, pig, dog, and cat is a single process preparatory to swallowing. The dog and cat chew very little, usually bolting their food in relatively large pieces.

In the ruminants, represented by the ox and sheep, this process is divided into two phases: (1) Preliminary or incomplete mastication when the food is first taken, and (2) complete mastication, which is postponed for more leisurely performance. The ruminant is unique among animals in being equipped with a partitioned stomach consisting of four compartments (fig. 2). These are known as the rumen, paunch, or first stomach; the reticulum, honeycomb, or second stomach; the omasum, manyplies, or third stomach; and the abomasum or rennet, the true or fourth stomach. The food material, which is usually of a coarse nature, after being partly chewed enters the paunch or rumen, from which it is later regurgitated or returned to the mouth and re-chewed in individual boluses during repose. This process of rechewing is known as rumination. Each bolus of food brought up for rumina-
tion is chewed for somewhat less than a minute. Grains form a part of the bolus only to the limited extent that they are accidentally caught in the roughage. Consequently, all unchewed grain passes through the animal and appears in the feces in an intact condition. In cattle a certain quantity of whole grain is not crushed during eating and rumination, and on this account grain is commonly ground for cattle. This is rarely done for sheep, which chew most grains very thoroughly. In ruminants the mucous membrane lining the cavity of the mouth is thicker than that of the horse and is furnished with many horny protuberances, known as papillae, which facilitate the manipulation of food during mastication.

The exceptionally mobile tongue of the ox has a groove across the upper surface a few inches back of its tip. This groove is frequently the seat of injury caused by sharp spines, awns, etc., in forage eaten by cattle. The injury is not a simple wound, and in most cases it results in the formation of a chronic ulcer with slight tendency to heal. Although many types of the common wound-infection micro-organisms are found in the lesion, actinobacilli and actinomyces fungi are most often encountered and certainly cause the most damage. The latter organisms are responsible for the so-called "wooden tongue" of cattle. Because of this peculiar anatomy of the cow's tongue with its susceptibility to injury, care should be exercised to exclude from the feed as much as possible all sharp, spiny substances.

THE SALIVARY SECRETION AND SWALLOWING

Mastication and the presence of food in the mouth cavity stimulate the secretion of saliva in the mouth in all mammals. In man the principal constituent of this secretion is a substance known as ptyalin, or salivary amylase, which functions in the digestion of starchy substances, but of the domestic animals only the pig possesses enough ptyalin in its saliva to be of importance in digestion. The salivary secretion in most domestic animals serves mainly to lubricate the food for swallowing. In ruminants the presence of saliva in the paunch assists in the regurgitation of partially masticated food for rechewing. In digestion by ptyalin or salivary amylase, the starch is first changed to soluble starch and finally to maltose.

Deglutition is the act of swallowing the food that has been taken into the mouth. It is accomplished by a series of muscular movements involving principally forcing the food to the rear of the mouth cavity by elevation of the fore part of the tongue and depression of the root of the tongue, followed by the dilatation of the pharynx. The bolus then passes through the pharynx and esophagus into the stomach. The initial phase of the act of deglutition, that relating to its passage into the esophagus, is entirely a voluntary process, but the completion of the act is involuntary.

The quantity of food material that can be swallowed at one time is comparatively small in the horse on account of the narrow lumen, or space between the walls of the pharynx and the esophagus. A much larger bolus can be swallowed by the ox, whose deglutitive organs are of more ample proportions. Nevertheless, ruminants frequently choke on apples, beets, turnips, and other pieces of food that have not been chopped fine enough for ready swallowing with little chewing.
There is no special or unusual factor involved in the swallowing process on the part of the pig, dog, cat, or fowl.

Fluids are swallowed in much the same way as solids, except that they are passed into the esophagus and stomach with extreme facility and rapidity as compared with solid boluses.

**DIGESTION**

In general the processes of gastric digestion are similar for all domestic animals. In the horse, pig, dog, and cat, the food material passes into the stomach as soon as it is swallowed and is there brought into immediate contact with the digestive fluids of the stomach—principally pepsin and hydrochloric acid. The fluids are mixed with the food by churning movements of the organ.

The action of bacteria upon food taken into the stomach of the horse, pig, or dog is short-lived owing to the rapid production of hydrochloric acid there. In the ox and other ruminants, however, considerable bacterial action is exerted upon the enormous amount of material taken into the capacious rumen prior to its regurgitation, remastication, and digestion. This bacterial action is favored by the slightly alkaline reaction of that portion of the stomach and its freedom from gastric secretions, as well as by the prolonged sojourn of food matter therein. The changes brought about by bacteria inhabiting the alimentary tract include the breaking up of cellulose and fats, the production of organic acids such as acetic, butyric, and lactic, and the splitting of the carbohydrates known as polysaccharides. The gases, methane, carbon dioxide, hydrogen, etc., are formed during bacterial action in the rumen, but they are of no value to the animal and are excreted as waste.

The first three stomachs of the ruminant are essentially for the purpose of storing and grinding the food material, true digestion taking place largely in the fourth stomach (the abomasum), and finally in the intestine.

The stomach of the horse is comparatively small. According to Dukes (285) it has been estimated that a horse may swallow during a given meal two or three times the amount of material (food and saliva) remaining in the stomach at the close of the meal. The excess, together with the food remaining from the previous meal, must pass on into the intestine during the meal, the first food consumed being in general the first to pass out. This consideration means that a good deal of the food cannot remain long in the stomach and raises the question of the importance of stomach digestion in the horse.

The true stomach of the ox or sheep is also comparatively small and receives food gradually in a well-macerated or ground-up condition from the first three stomachs. The stomach of the pig, dog, or cat is sufficient in size to contain all the food that may be consumed at a meal, and food may be retained in the stomach for a considerable time. In all mammals the food is mixed and softened in the stomach by muscular movements, assisted by the action of the gastric juice. The softer portions of the food material thus prepared are then passed into the intestine, but food not ready for intestinal digestion is not allowed to pass from the stomach, with the exception of whole grain in cattle.

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2 Italic numbers in parentheses refer to Literature Cited, p. 1075.
Fowl, having no teeth, must swallow their food whole or at best only coarsely broken by the beak at prehension. Such material passes through the pharynx and esophagus into the crop (fig. 5), which in most avian species is nothing more than a dilated portion of the esophagus. The purpose of the crop of the fowl, like that of the rumen of the ox and sheep, is largely bulk storage of food. This material then passes by slower stages into the proventriculus, or glandular stomach, a specialized gastric organ of small capacity whose wall is furnished with secretory glands supplying pepsin and hydrochloric acid. The food material after coming into contact with these digestive fluids continues on its way into the gizzard, or muscular stomach. That organ is lined with a tough membrane and is so constituted that it retains a certain portion of the grit normally swallowed by the fowl. The food substance is somewhat softened by the time it reaches the gizzard, where it is subjected to crushing contractile movements stimulated by the presence of food. The food substance is reduced to a very fine consistency by the rubbing together of the grit and the tough, corrugated lining of the organ. This process corresponds to mastication. Strictly speaking, there is no true gastric digestion in the fowl, such as is common to mammals. The food material after being finely divided in the gizzard is passed on into the first portion of the small intestine, where it is more thoroughly mixed with and digested by the juices derived from the proventriculus as well as the other digestive enzymes emptying into the intestine.

The alimentary tract of the chicken is for the most part representative of those of the majority of species of domesticated fowl, but there are some minor differences.

The pigeon is peculiar in not possessing a gall bladder, and in having ceca that are small and poorly developed as compared with those of the duck and chicken. Neither the duck nor the pigeon possesses a true crop comparable to that of the chicken, but in these species there is a specialized enlargement of the esophagus which serves the purposes of the crop. The small intestine of the pigeon is shorter in proportion to the size of the bird than that of the duck or the chicken.

The pigeon is also peculiar in being specially equipped to nourish its young by regurgitating into the mouth of the squab a milklike substance secreted in the "crop." The mechanism by which this substance is secreted is as follows: Beginning about the eighth day of incubation of the eggs, the cells of the mucous membrane of the crop in both the female and the male birds increase in size and number. These cells, which contain considerable quantities of fat, secrete fat globules into the crop during the course of incubation in much the same manner as the cells of the mammary glands of mammals act in the secretion of milk. There is also a constant shedding of these cells, which then form a part of the milklike substance. At the time of hatching of the eggs, an abundance of "pigeon milk" is ready for feeding the squabs. The secretion of the milk continues until about the twentieth day after hatching.

The following composition has been determined for this curious lacteal secretion: Dry matter, 14 to 25 percent; fat, 25 to 29 percent; protein, 13 to 14.5 percent; calcium, potassium, magnesium, and phosphorus (in the ash); no sugar; enzymes; amylase; and saccharase.
Figure 5.—The digestive tract of the fowl (after B. F. Kaupp, The Anatomy of the Domestic Fowl). Capacity of gizzard, 0.089 pound. Length of proventriculus, 1.62 inches; diameter of glandular stomach (proventriculus), 0.8 inch. Length of small intestine, 61.7 inches; of ceca, 7.6 inches each; of large intestine, 4.6 inches.
The striking features of pigeon milk are its high fat and protein content and the absence of sugar. In this respect it resembles the milk of the rabbit. Young rabbits stand out as having the most rapid rate of growth among mammals, and the pigeon holds the record among birds for rapidity of growth during the first 20 days after hatching. The squab doubles its weight within 48 hours after hatching, while the duck requires 6 days and the chicken 9 days. In 20 days from hatching, a squab has shown an increase in weight from 20 to 435 grams.

There is evidence that a hormone, prolactin, an internal secretion of the anterior pituitary gland located at the base of the brain, is the inciting agent of pigeon milk. Injection of prolactin into pigeons produces the effect described in the membrane lining of the crop. Moreover, the injection of this substance into castrated male pigeons 6 months after castration engendered a secretion in the crop.

Sometimes the death of the squabs and the consequent failure to use the secreted material results in a congestion of the crops of the parent pigeons. Such a condition is best overcome by furnishing another squab for the pair to nurse.

In the horse, ox, sheep, and pig, well-ground and softened food in the stomach undergoes gastric digestion through the action of the pepsin and hydrochloric acid of the gastric juice. In the dog and cat, in which mastication has been eliminated to a large extent, the food in the stomach is subjected to the same process as in the other animals but for a longer period.

Digestion by the gastric juice is essentially the same in all animals (fig. 6). The pepsin of the gastric juice in the presence of hydrochloric acid acts upon proteins of either animal or vegetable origin and converts native protein into the simpler products, proteoses and peptone. The latter substances are not yet ready for absorption but require further conversion into amino acids. This step in protein digestion remains to be completed in the intestine.

Another digestive enzyme sometimes known as rennin is present in the gastric juice of young mammals. This enzyme coagulates milk so that the casein is prevented from too rapid passage through the stomach and the pepsin is enabled to convert it into proteoses and peptone. In all species, following gastric digestion the semiliquid substance is passed into the small intestine; at this point it is known as chyme. Digestion by pepsin occurs largely in the stomach, but it is continued to some extent in the first part of the small intestine.

In the intestines the chyme undergoes further digestion by the action of pancreatic juice, intestinal juice, and bile. The pancreatic juice contains three important enzymes—trypsin, steapsin, and amylopsin. To a limited extent trypsin, like pepsin, converts native protein into proteoses and peptone. Principally, however, it continues the digestion of protein where the pepsin leaves off, that is, breaks the proteoses and peptones into the amino acids, which can be absorbed. The steapsin breaks down or hydrolyzes fats into fatty acids and glycerol, in which forms they are ready for absorption. Some of the fatty acids resulting from steapsin digestion combine with the available alkali in the intestinal juice to form soaps which assist in emulsifying any remaining undigested fat. The amylopsin
<table>
<thead>
<tr>
<th>FOOD</th>
<th>ENZYME</th>
<th>SECRETING GLAND OR ORGAN</th>
<th>STEPS IN THE BREAK-DOWN</th>
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<td>MALTOSSE</td>
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<td>INTESTINE</td>
<td>SAME AS PANCREATIC LIPASE</td>
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\(^1\) ONLY THE PIG, DOG, AND CAT HAVE THE SALIVARY AMYLASE.

\(^2\) THE PANCREATIC LIPASE IS MOST IMPORTANT, THE GASTRIC LIPASE BEING OF LITTLE PHYSIOLOGICAL IMPORTANCE.

Figure 6.—The break-down of various food elements in the digestive system and the enzymes involved.
converts or hydrolyzes starch and the dextrines into maltose. Maltose requires further breaking up by other digestive juice before it is ready for absorption.

The intestinal juice contains a number of digestive enzymes, for example, enterokinase, erepsin, maltase, sucrase, lactase, lipase, amylase, and nucleinase. Enterokinase is largely concerned in the activation of the enzyme trypsin of the pancreatic juice. Erepsin, which is a proteolytic enzyme—that is, one that has the power to break down proteins into simpler diffusible substances—converts peptones and peptids into amino acids. Maltase converts the maltose resulting from the action of amylolysin on starch into glucose, in which form it can be absorbed. Sucrase breaks down or hydrolyzes sucrose into glucose and fructose, in which forms they are assimilated. Lactase, which is present only in young mammals ingesting milk, converts lactose (milk sugar) into glucose and galactose. This enzyme is lacking in mature animals that do not consume milk as food. However, it is reported that lactase can be made to recur in adult animals fed milk or lactose. Lipase is the same as steapsin and converts fats into fatty acids and glycerol. Amylase hydrolyzes starch. Nucleinase converts nucleoproteins into protein and nucleic acid.

Bile is a highly complex fluid formed in the liver. It is not an enzyme but plays an important role in the digestion of fats. The flow of bile into the intestinal tract is more or less continuous, but it increases after the entrance of food into the stomach. Its quantity is governed by the amount and character of the food received. The elaboration and storage of bile in the liver and its release into the intestinal tract are not the only or the most important duties of the liver, but the other functions of that organ have no place in this discussion. The principal constituents of bile are bile pigments, bile salts, and cholesterol. The bile salts only are concerned in the digestive process. They aid digestion by activating the pancreatic lipase, enhancing the action of pancreatic amylase, emulsifying fats, and increasing the solubility of fatty acids and their soaps so that they may be ready for absorption. Bile also is necessary for the absorption of the fat-soluble vitamins. Bile being a reservoir of alkali helps to maintain the alkaline reaction so necessary for pancreatic intestinal digestion.

In addition to the enzymes secreted by the various organs, there are, particularly in the digestive tracts of herbivores and omnivores, bacteria which break down cellulose into substances that can be absorbed and used by the animal organism. This bacterial activity is of considerable importance, since the vegetable substance consumed in large quantities by the horse, ox, sheep, and pig contains a large proportion of cellulose, which is not digested by the enzymes in the various digestive juices. This bacterial digestion makes available for utilization by the body large quantities of otherwise indigestible food material.

**ABSORPTION**

The digestive processes by which carbohydrates and fats are broken down into soluble or emulsified forms ready for absorption have been
described. The inorganic salts, water, and vitamins contained in food require no breaking down but are absorbed as such. The end products of protein digestion are amino acids. Carbohydrates are broken into simple sugars (monosaccharides), principally glucose. The end products of cellulose digestion are probably the simple fatty acids (acetic and butyric) and glucose. The fats are broken down into fatty acids and glycerol. The absorption of all of these food elements occurs chiefly in the small intestine, though some absorption occurs in the large intestine also, particularly in the horse.

The principal avenues of absorption of food are the myriads of microscopic protuberances from the mucosa, or lining membrane of the intestinal wall, known as villi. These minute, fingerlike structures are composed of an outer layer of absorbent cells, a wall containing many blood vessels, and in the center a lacteal or lymphatic vessel. Being in constant contact with the food in a digested state, the villi take up the digested fats and pass them through the lymph channels (commonly known as lacteals) into the blood stream. The lymph within the lacteals is a milky substance heavily laden with the digested fat and is known as chyle. The end products of protein and carbohydrate digestion, inorganic salts, water, and vitamins enter the blood vessels of the villi direct and are transported through the liver into the blood system of the body. These absorbed food substances are carried to the body tissues, where after having undergone complex metabolic processes they are utilized for growth, repair, and energy.

After the digestive tract has taken from the food all the nutritive elements of value to the animal, the remaining material is excreted as waste (feces).