

ALIMENTARY SYSTEMS IN SOME HOMEOTHERMIC VERTEBRATES

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Summary

The alimentary systems of animals vary greatly. The carnivores have short gastrointestinal tracts, which work fast, and herbivores have longer and more elaborate systems. Cows as cranial fermentors have remarkable ability to utilize different plant feeds with the aid of their rumen and its microflora. One cow can produce milk in quantities up to some 20 tons per year. Cranial fermentors can also handle significant quantities of poisonous materials with the help of their microflora before the toxins are absorbed in the small intestine. Caudal fermentors like horses are more sensitive, both to changes in their feed and its toxic components, as the microflora works mostly after the small intestine. Some of the caudal fermentors like guinea pigs and rabbits form special feces, which they eat to benefit from the valuable microfloral products. Birds also form a special group as their capacity to store energy is limited due to weight problems. Their alimentary system must work fast, as maintaining a low weight is critical for both flight and escape. The high body temperature of mammals and birds also mean high energy consumption, and their abilities to fast are more limited than poikilothermic species like snakes. One must, however, remember that species like dogs

need fasting periods and regular overfeeding with limited exercise possibilities may cause similar problems as humans suffer, i.e. metabolic and cardiovascular diseases.

1. Introduction

Vertebrates are classified into six classes: *Cyclostomata*, *Pisces*, *Amphibia*, *Reptilia*, *Aves* and *Mammalia*. Their digestive canals differ considerably from each another, as does what they eat. They also vary greatly according to their developmental level and ecology. Mechanical, chemical and microbial methods are used to break down the food items to molecules that can be absorbed. The teeth and beak, as well as the gizzard in birds, are responsible for much of the mechanical tasks. Enzymes catalyze the hydrolytic reactions. Microbes are responsible for fermentation in digestion.

Foods are propelled through the digestive system and mixed with enzyme-rich digestive juices, which are secreted in response to specific stimuli. Enzymes of ingested materials (if not cooked) as well as microbes and microbial enzymes, also have important roles in digestion. Fermentation takes place in all species, but especially in herbivores.

One must remember that in many species, including humans, high hydrochloric acid concentration slows down the action of food enzymes and denatures most of them. Pepsins also break them down.

Digestion hydrolyzes (i.e. breaks the chemical bonds by the addition of water) the polymers in the food into molecular components. They cross the plasma membrane of enterocytes with the aid of specific mechanisms and after absorption the blood distributes them to different tissues (see *Enzymes of Digestion*).

Carbohydrates are mostly glucose polymers hydrolyzed by amylases and disaccharidases. Proteins are polymers of amino acids linked together by peptide bonds. Enzymes that hydrolyze proteins and peptides to amino acids are called proteases and peptidases. The most abundant energy storage form is neutral fat or triglycerides in animals and plants, and hence the most important dietary lipids are triglycerides. They are hydrolyzed by lipases. Fatty acids possess a long hydrocarbon chain terminating in a carboxyl group. The principle differences among the many fatty acids are the length of the chain (usually 16 or 18 carbons) and the positions of double bonds in unsaturated fatty acids. Short chain fatty acids are water (and blood) soluble, but the long chain fatty acids are reconverted to triglycerides in the gut mucosa and travel in protein-covered chylomicrons via the lymphatics to the blood stream.

Polysaccharides are the most abundant dietary carbohydrates for most animals, except very young milk-fed mammals, which receive disaccharide lactose. Most polysaccharides are large polymers of glucose. Starch is the main plant storage form. It occurs as alpha-amylose, in which the glucoses are linked together in straight chains, and amylopectin, in which the chains are branched. Except for the branch points of amylopectin, the glucose monomers in starch are linked via alpha (1->4) glycosidic bonds. Glycogen is the third large polymer of glucose, and it is the major animal storage carbohydrate. It has similarities with amylopectin.

More than half of the organic carbon on Earth is, however, found in cellulose. Cellulose is the major constituent of plant cell walls. It is composed of unbranched, linear chains of glucose molecules, linked to one another by beta (1->4) glycosidic bonds. No vertebrate has the capability to digest it with its own enzymes. Herbivores subsist largely on cellulose, and in their digestive tract the microbes produce the necessary cellulases for its hydrolysis.

The purpose of this overview is to briefly describe the main characteristics of the digestive systems of some homeothermic vertebrates. The examples have been selected from species which are common, and important as companion and production animals and thus more-or-less well known to all readers, but whose digestive systems have special features to meet the needs of their natural diets. Sometimes people forget or do not know their specifics and problems occur. Poikilothermic animals are not discussed as they can fast for long periods and their feeding permits long pauses—a feature which is helpful to pet owners.

2. General Structure of Digestive Tract

The digestive apparatus consists of the alimentary canal and its accessory organs. It receives, stores and digests the food, passes it through the body and expels the unabsorbed material in feces, along with the bile (in birds also in the urine), excreted waste components and microorganisms. The alimentary canal has functionally specialized parts from the lips and teeth (missing in birds) to the anus: the mouth, pharynx, esophagus, stomach, small intestine, large intestine with cecum, rectum and anus. It has a complex mucous membrane with highly specific enterocytes and an external muscular coat. This tube is largely covered with a serous peritoneum. The teeth, tongue, salivary glands, liver, gall bladder (not in all species) and pancreas are the accessory organs.

Digestive functions are regulated by the combination of nervous and hormonal messages. They mostly originate within the digestive system itself. The central nervous system and endocrine organs such as the adrenal gland contribute, however, to their regulation and integrate the information received from the whole body.

From the mouth to the anus, the wall of the digestive tube is composed of four layers. Most part of the digestive tract (stomach and intestines) is covered by a thin loose connective tissue and by squamous epithelium that lines body cavities (mesothelium). In the abdominal cavity, the serosa on each side of the tube fuses together to form a suspensory mesentery. This supplies vessels and nerves to the digestive tract. In regions outside of the abdominal cavity the digestive tube is affixed to adjacent structures via its outer layer of connective tissue (esophagus and rectum).

The mucous membrane is the innermost layer of the digestive tube. Of the four layers, the mucosa is the most variable in function. It performs digestive tasks and takes care of absorption, but it is also an endocrine organ. These hormones act locally, but they also contribute to the general humoral regulation of the body. The epithelial cells are in direct contact with the luminal chyme and its bacterial flora. Therefore the gastrointestinal mucosa is an important site of the immune defense system. The mucosal

sheet is distinctly different in different regions of gastrointestinal the tract. Several different cell types contribute to secretion, digestion and absorption as well as to the production of hormones and contributors to the immune system.

The intestinal epithelium lies on the *lamina propria*—connective tissue through which the blood vessels and lymphatics supply the epithelium. This layer also contains lymphatic nodules important to immune functions of the digestive tract. Under the lamina propria there is a thin smooth muscle (*lamina muscularis mucosa*). This permits the mucosa to move and fold.

Beneath the mucosa, the dense connective tissue contains blood and lymphatic vessels as well as the submucous nervous plexus, which controls the mucosal functions.

The *tunica muscularis* is responsible for peristalsis and other motilities in the gastrointestinal tract. In most parts of the digestive tube, it consists of two thick layers of smooth muscle. Muscle fibers in the inner layer are circular but in the outer layer they are longitudinal. The circular and longitudinal smooth muscles mix the gut contents with enzymes and propel chyme in the lumen. Between the inner circular and outer longitudinal layers of smooth muscle, the myenteric plexus regulates the motions.

2.2. Mouth

The mouth with its muscularous lips and teeth (both missing in birds, which have a beak) is adapted for mechanical food intake and chewing. In meat eaters (carnivores) the teeth hold, cut and chew the prey. Many reptilians have poison producing glands in the mouth to paralyze the prey. In herbivores the molar teeth are larger for chewing fibrous plants. In herbivores the tongue helps in capturing the grass and passing it into the mouth. It pushes the chewed bolus towards the pharynx to be swallowed. Mammals have taste buds in their tongues but birds less.

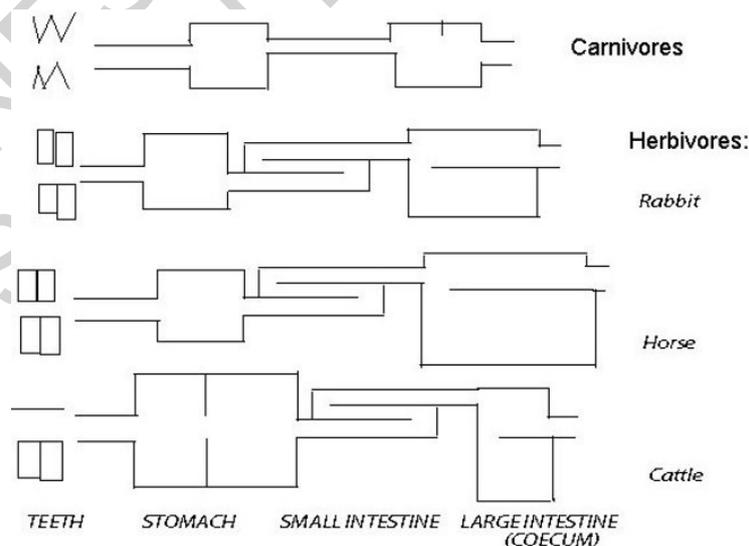


Figure 1. Schematic description of the homeothermic vertebrate gastrointestinal tracts. Carnivores have shortest and simplest structures and fast digestion. Herbivores have

more complicated and voluminous structures. Cattle and other ruminants have most elaborate systems, as they are cranial fermentors. The fermentation continues also in the cecum and large intestine. Horses are caudal fermentors with voluminous cecum.

Rabbits are also caudal fermentors, but they also form special feces, which they eat themselves. Horses may also, but less often, eat their feces.

The *salivary glands* lubricate and moisten the food, enhancing swallowing. In many animals saliva contains enzymes such as ptyalin-amylase, which starts the breakdown of starch into dextrins and maltose. Salivary bicarbonate neutralizes the acids in food. The mouth fluid also contains antimicrobial agents. Licking wounds may thus help in their healing. Similar agents exist also in humans. Figure 1 is a schematic illustration of the gastrointestinal tract of some mammals. Carnivores have simple and short gastrointestinal tracts, and herbivores more complicated and relatively long ones.

2.2. Stomach

The swallowed food enters the stomach through the esophagus, and the stomach wall musculature then mixes the food into watery mucus-rich chyme. Gastric epithelial glands secrete hydrochloric acid (pH 1.5 to 3), which kills the microbes and helps to activate pepsinogen into pepsin, which starts the protein hydrolysis. The stomach receives both parasympathetic (vagal nerve) and sympathetic fibers of the autonomous nervous system. The stomach also releases hormones such as gastrin.

In ruminants the structure and functions of the stomach complex is remarkably specialized, as described later (see Figure 2).

2.3. Intestine

The small intestine is relatively short in carnivores and long in herbivores, (some 8 m in humans and 30 m in a cow). The total length of the digestive canal varies from 2 to 25 times the body length.

The acid fluid chyme from the stomach is mixed in the duodenum with alkaline pancreatic secretion, intestinal fluid and bile. The intestine with its enlargements, sacs, folds, and microvilli enlarge the absorption surface and prevents the chyme flowing too fast. Hormones released by the small intestine regulate the functions of the stomach, liver and pancreas in addition to the local effects (see *Endocrinology*).

Peristalsis propels foodstuffs through the esophagus and intestines. There is contraction above and relaxation below the segment being stimulated. Peristalsis is controlled by the intestine's intrinsic local nervous system. Distension and perhaps mucosal irritation stimulate afferent enteric neurons. One group of interneurons activates excitatory motor neurons above the bolus by acetylcholine and substance P. This ends in contraction of smooth muscle above the bolus. A second group of interneurons activates the inhibitory motor neurons that cause the relaxation below the bolus by using nitric oxide, vasoactive intestinal peptide (VIP) and ATP as transmitters.

Bile emulsifies the alkalized chyme by diminishing the surface tension. It thus helps the pancreatic lipase and phospholipases, hydrolyzing fats into mono- and diglycerides, glycerol and fatty acids and also to components of the phospholipases. The pancreatic trypsin, chymotrypsin and carboxypeptidases hydrolyze proteins into peptides and amino acids. The intestinal wall contains membrane bound amino- and dipeptidases, which continue the work by hydrolyzing peptides to amino acids ready to be absorbed. Pancreatic starch splitting amylase continues the hydrolytic action of salivary amylase on starch and glycogen. Enterocyte surface maltase, lactase and saccharase decompose disaccharides to monosaccharides.

The small intestine is the main site of absorption of nutrients. Carbohydrates are absorbed as monosaccharides, proteins as amino acids and short peptides and fats as glycerides, glycerol and fatty acids. The longer fatty acids enter the lymphatic pathways in the form of chylomicrons and thus pass the hepatic portal vein and are transported directly via the thoracic duct to the upper vena cava and hence into the general circulation.

In the cecum and multilocular colon (1 to 1.4 m in humans and 10 m in the cow) water is absorbed and the rich bacterial flora attacks the ingesta by decomposing it for their own growth. For example cellulose and hemicelluloses are hydrolyzed (see sections 3.3 and 4.4) and short chain fatty acids and water-soluble vitamins are synthesized. Bacterial proteins will mostly be lost in monogastric “caudal fermentors” (see Horses) but not always (see Rabbits). The undigested food and waste substances are excreted through the rectum and anus in the form of feces.

In monogastric omnivores some 60 to 90% of the nutrients in the eaten foods are digested. In herbivores eating more fibrous feed the digestibility is lower i.e. 50 to 70%.

2.5. Liver and Pancreas

The liver is one of the largest organs in the body. It is situated caudal side to the diaphragm.

Liver is able to convert glucose, amino acids, propionic acid and other substances into glycogen. All energy substrates can be converted to acetic acid and finally to longer fatty acids and triglycerides as well as to steroids like cholesterol. The decomposition of red blood cells is completed in the liver, and the iron released from the hemoglobin is stored. Liver makes bile pigments when red blood cells are broken down. These pigments are excreted in the bile. The liver also produces bile salts, which have an important role in the emulsification and absorption of fats. It is stored and concentrated in the gall bladder. Not all animals, however, have a gall bladder. One such example is the rat. Bile is discharged through the bile duct into the duodenum, when the chyme arrives. Bile salts are reabsorbed and return to the liver.

Excess amino acids cannot be stored, and they are converted into carbohydrates and/or fatty acids by the removal of their amino group. Liver can also synthesize some of the amino acids. Some must be obtained from the food. The nitrogen from amino groups is

finally converted to urea and is excreted in urine via the kidneys. Liver also synthesizes most of the proteins found in blood plasma.

When fats stored by the body are required for energy production, they travel in the blood stream. Some are used directly, but some are oxidized by the liver to ketoacids (ketones), which can be oxidized by other tissues. The fat-soluble vitamins A, D, E and K are stored in the liver. It also stores vitamin B12.

Detoxification of toxins in the feed and those produced by bacteria in the large intestine, takes place in liver. Amino acids are the starting material e.g. to phenols in bacterial metabolism. The xenobiotics are converted by the liver into harmless conjugates for excretion either in urine or bile.

The pancreas lies next to the stomach. Two types of tissue are present in the pancreas. They have very different functions. Exocrine pancreatic juice consists of sodium bicarbonate and various enzymes capable of hydrolyzing all major components eaten, except cellulose. The endocrine islets produce hormones such as insulin and glucagon. Insulin is produced in the beta cells of the islets, and it stimulates the glycogen formation in muscles and liver from blood glucose.

2.6. Microbes Contribute to Digestion

The numbers of bacteria in the gastrointestinal tract vary by region and animal species. In healthy humans the stomach and proximal small intestine contain few microorganisms, largely as a result of the bacteriocidal gastric acid. Those that are present are aerobes and facultative anaerobes (see Table 1).

	Stomach	Jejunum	Ileum	Colon
Viable bacteria per gram	0 - 10 ³	0 - 10 ⁴	10 ⁵ - 10 ⁸	10 ¹⁰ - 10 ¹²
pH	3.0	6.0-7.0	>7.5	6.8-7.3

Table 1. Microbial numbers in the digestive tract of normal humans.

In contrast to humans, in most animals the stomach and also the proximal small intestine house a rich microbial flora. In ruminants the microflora actually does most of the digestive work on hay before it reaches the gut. The contents of the colon literally teem in all vertebrates with predominantly strict anaerobic bacteria. In herbivores such as the horse, the cecal microflora does much of the hay digestion. Between these two extremes is a transitional zone, usually in the ileum, where moderate numbers of both aerobic and anaerobic bacteria are found (see *Nutrition and Digestion*).

The gastrointestinal tract is sterile at birth, but microbial colonization begins within a few hours after birth. In humans, an adult type microbial flora is established by two years of age i.e. comparatively slowly with the dietary shift from mother's breast milk to adult-type diet.

Microflora contributes to the morphology of the intestine. In germ-free animals it differs considerably from normal conventional animals housing a rich microflora. In germ-free animals the rate of epithelial cell renewal is slow and, as one would expect, the number and size of Peyer's patches contributing to the immune responses are reduced. On the other hand the cecum of germ-free rats is roughly 10 times the size of that in the conventional rat.

Bacteria in the intestinal lumen metabolize a variety of steroids. For example, bacteria reduce the bile salt cholic acid to deoxycholic acid. Small intestinal bacteria also have an important role in sex steroid metabolism.

Finally, bacterial populations in the large intestine digest carbohydrates (also cellulose), proteins and lipids that have escaped digestion and absorption in the small intestine. Microbial fermentation of complex carbohydrates including cellulose is of critical importance to herbivores, but it also has some significance in humans.

3. Carnivores

Carnivores have sharp teeth. The diastema is an occlusal gap for large protruding canine teeth. The gap allows the jaw to close and function like scissors, as all the teeth are sharp. The canines lock together to hold captured animals. Carnivores have the simplest and shortest gastrointestinal tracts compared to herbivores and omnivores (see Figure 1). Carnivores eat irregularly, fast often, and have little choice in this matter, as success in catching prey varies.

The enzymatic digestion of proteins is initiated in the stomach by pepsins and foodstuffs are reduced to liquid chyme. The small intestine has a central role in the entire digestive system. The final stages of enzymatic digestion take place there and almost all nutrients are absorbed. The exocrine pancreas provides a potent mixture of digestive enzymes to the small intestine.

Water is, however, absorbed in the large intestine in all animals. Bacterial fermentation is limited in carnivores as they eat little cellulose and other fibers.

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Biographical Sketches

Seppo Haaranen, veterinarian, assessor, was born in 1928 in Sortavala, Finland. He studied at the Universities of Helsinki, Finland and Stockholm, Sweden, where he received his degree of Doctor of Veterinary Medicine in 1952, and Licentiate of Veterinary Medicine in 1961. He has served as assisting teacher of pharmacology in the Veterinary College, Helsinki, lecturer in the University of Kuopio, Finland and as a municipal veterinarian and regional veterinarian, as well as laboratory director.

He has contributed to a number of papers in refereed journals. He was, for example, the first to describe the role of selenium in the heart morbidity and mortality in farm animals. He has been an especially active author of papers on practical topics in the Finnish Journal of Veterinary Medicine.

Dr Osmo Otto Päiviö Hänninen, DMS, Ph.D., Professor of Physiology, Emeritus, Finland. Born 1939, Lahti, Finland. He studied at the University of Helsinki and the University of Turku, Finland, where he received his Master of Sciences (Biochemistry) in 1962, Licentiate of Medicine (MD) in 1964, Doctor of Medical Sciences (DMS) in 1966, and passed his dissertation in biochemistry for his Ph.D. in 1968. He has also studied genetics. He has been a specialist in sports medicine since 1986. He served as the Research Assistant of Professor K. Hartiala, 1962–4; Assistant of Physiology, 1964–5; Laborator of Physiology, 1966–7; Docent of Physiology, from 1967, and Associate Professor of Biochemistry, 1969–71, at the University of Turku; Acting Professor in the Planning Office, 1971–2; and from 1972, Professor of Physiology and Chairman of the Department of Physiology, University of Kuopio; Vice-President of the University of Kuopio, 1972–9; and President, University of Kuopio, 1981–4. Furthermore, he served as Visiting Professor of Physiology at Shanghai Medical University, China, 1991–2, and at Sun Yat Sen Medical University, Guangzhou, China, 1998–9; as Foreign Member of the Russian Academy of Natural Sciences, from 1994; and as Secretary General, International Council for Laboratory Animal Science, 1988–95. He was the President of Societas Physiologica Finlandiae, 1990–9, and has been President of the International Society for Pathophysiology and a Member of the Executive Committee since 1994, and the Treasurer of the International Union of Biological Sciences since 1997.

His special interests in research are:

1. - Biotransformation and adaptation to chemical loading, biomonitoring of toxicants, and comparative biochemical toxicology.
2. - Muscle metabolism and function.
3. - Ergonomics.

He has contributed 266 papers in refereed journals and seventy-two in proceedings, and written fifty-five reviews, and thirty books or book chapters. He serves on the editorial board of four international journals and is at present the European Journal Editor of *Pathophysiology*.

Of his post-graduate students (thirty-two in biotransformation, twenty-seven in muscle metabolism and physiology, and five others), twelve serve as professors in China, Finland, Greece, Sweden, and the United States.