

Digestive system

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The vertebrate digestive system consists of the digestive tract and ancillary organs that serve for the acquisition of food and assimilation of nutrients required for energy, growth, maintenance, and reproduction. Food is ingested, reduced to particles, mixed with digestive fluids and enzymes, and propelled through the digestive tract. Enzymes produced by the host animal and microbes indigenous to the digestive tract destroy harmful agents and convert food into a limited number of nutrients, which are selectively absorbed. The digestive systems of vertebrates show numerous structural and functional adaptations to their diet, habitat, and other characteristics. Carnivores, which feed exclusively on other animals, and species that feed on plant concentrates (seeds, fruit, nectar, pollen) tend to have the shortest and simplest digestive tract. The digestive tract tends to be more complex in omnivores, which feed on both plants and animals, and most complex in herbivores, which feed principally on the fibrous portions of plants.

Gut structure and function can also vary with the habitat and other physiological characteristics of a species. The digestive tract of fish has adaptations for a marine or freshwater environment. The hindgut of terrestrial vertebrates plays an important role in the conservation of the fluids, electrolytes, and nitrogen in the digestive secretions, and in the urinary excretions of reptiles and birds. Fish, amphibians, and reptiles are ectotherms, whose body temperature, metabolic rate, and nutritional requirements vary with their ambient temperature. The endothermic birds and mammals require a higher and more continuous input of nutrients for the maintenance of a constant body temperature. The basal metabolic rate per gram of body weight increases with a decrease in the body mass. Therefore, small animals must process larger amounts of food per gram of body weight, thus limiting their maximum gut capacity and digesta retention time.

Anatomy

Because of wide species variations, the digestive system of vertebrates is best described in terms of the headgut, foregut, midgut, pancreas, biliary system, and hindgut.

Headgut

The headgut consists of the mouthparts and pharynx, which serve for the procurement and the initial preparation and swallowing of food. Movable, articulated jaws are found in all vertebrates except the cyclostomes (lampreys and hagfish), which are primitive, parasitic fish. Teeth, used for grasping, cutting, or tearing of food, are located in the jaws or other

mouthparts of most fish. However, in some species, such as the chub, they are located in the pharynx and used as a grinding mill (**Fig. 1**), while the mouthparts of basking sharks and paddlefish are used for the filtering or sorting of food. Complex mechanisms for the microfiltration of ingested food are seen also in some species of larval amphibians, as well as flamingos and baleen whales. Some larval amphibians have horny teeth that are used for procuring prey or grazing on plants, but all adult amphibians are carnivores with a weak dentition that is used only for grasping and positioning prey. Most reptiles have teeth that are used for the procurement, cutting, tearing, or crushing of food, but turtles and birds use a beak for these purposes.

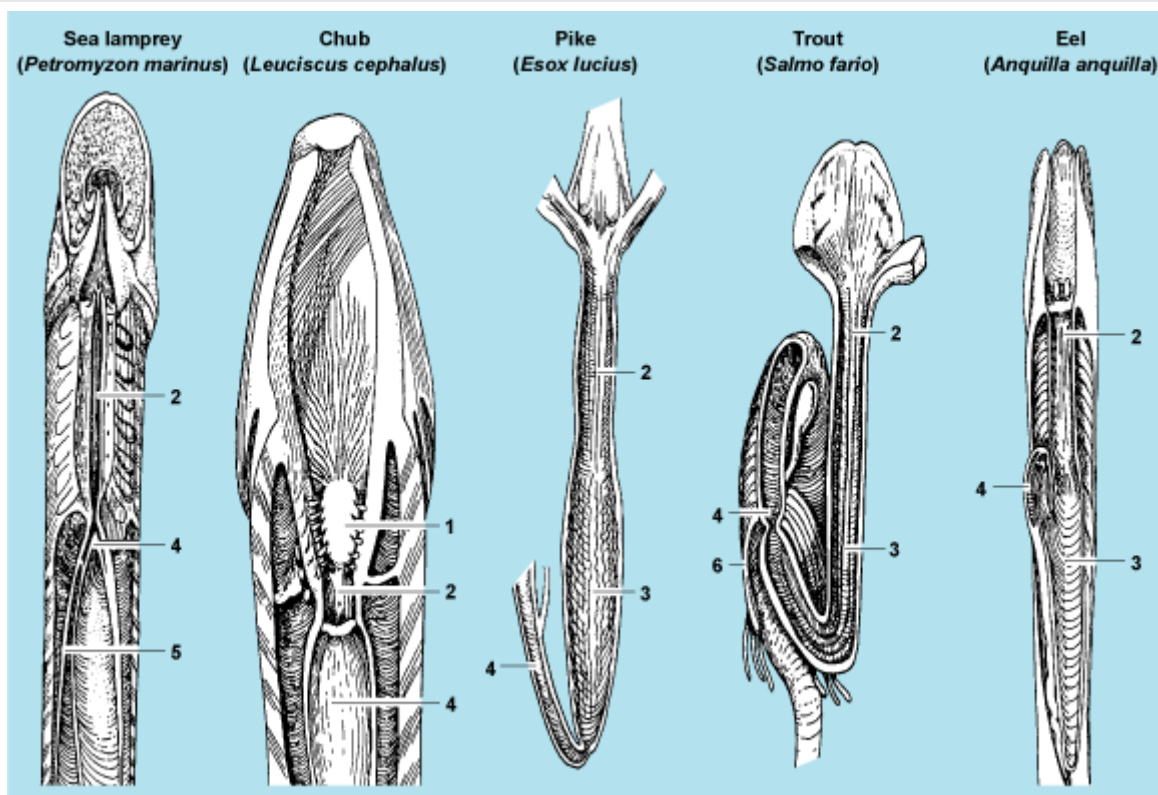


Fig. 1 Major variations in the foregut and midgut of fish. The teeth of most fish are located on the jaws or other mouthparts, but their location in the pharynx (1) of some species such as the chub allows mastication of food without the loss of fine particles through the gills. The esophagus (2) varies in length. The stomach (3) is absent in cyclostomes, such as the lamprey, and in some advanced species, such as the chub. Where present, it may be straight as in the pike, U-shaped like that of the trout, or Y-shaped with a gastric cecum, as seen in the eel. The intestine (4) tends to be relatively short with little distinction between the midgut and hindgut in most fish, but the lumen surface area and digesta retention time of the midgut are increased by a spiral valve (5) or pyloric ceca (6) in some species. (Modified from W. Harder, *Anatomy of Fishes, Part II, Schweizerbart'sche Verlagsbuchhandlung, 1975*)

A few mammals have no teeth. The ant and termite eaters in five mammalian orders have simple teeth and weak jaws. However, the teeth of most mammals consist of incisors and canines for grasping, cutting, and tearing, and premolars and molars with uneven occluding surfaces. The articulation and musculature of the mammalian jaws allows both the vertical movement of the lower jaw and either its lateral movement, as seen in most species, or the forward and backward movement, as seen in rodents and elephants. Thus, mammals have the unique ability to use their premolar and molar teeth for the grinding as well as the crushing of food. A movable tongue aids in the procurement of food by frogs, toads, woodpeckers, and mammalian anteaters, and for placement of food between the molars of mammals. Oral glands secrete adhesive materials in frogs, toads, woodpeckers, and mammalian anteaters, toxins in some reptiles, and fluids that aid in the deglutition or swallowing of food in reptiles, birds, and mammals. See also: [Oral glands \(/content/oral-glands/474100\)](#); [Tongue \(/content/tongue/700200\)](#)

Foregut

The foregut consists of an esophagus for the swallowing of food and, in most species, a stomach that serves for its storage and initial stages of digestion. The esophagus of most vertebrates is lined with a multilayer of cells that are impermeable to absorption. In most birds it contains the crop, an outpocketing of its wall that provides for the temporary storage of food. A stomach is present in all but the cyclostomes and some species of advanced fish (Fig. 1) and in the larval amphibians. In most vertebrates it consists of a dilated segment of the gut that is separated from the esophagus and midgut by muscular sphincters or valves. This is often referred to as a simple stomach. However, in birds these functions are carried out by the crop (storage), proventriculus (secretion), and gizzard (grinding or mastication). See also: [Esophagus \(/content/esophagus/242100\)](#); [Stomach \(/content/stomach/657200\)](#)

In most vertebrates, a major portion of the stomach is lined with a proper gastric mucosa (epithelium), which secretes mucus, hydrochloric acid (HCl), and pepsinogen. The distal (pyloric) part of the stomach secretes mucus and bicarbonate ions (HCO_3^-), and its muscular contractions help reduce the size of food particles and transfer partially digested food into the midgut. The stomach of reptiles and most mammals has an additional area of cardiac mucosa near its entrance, which also secretes mucus and bicarbonate ions.

The stomach of some mammals differs from that of other vertebrates with respect to its epithelial lining, structure, or size (Fig. 2). In some of the species belonging to 10 of the 20 mammalian orders, the cardiac mucosa is preceded by a region of stratified squamous epithelium, similar to that of the esophagus. This can vary from a narrow region, as seen in the pig, to one-half of the stomach, like that of the horse and rat, to a major fraction of the stomach, as seen in the ox and llama, to the entire stomach of monotremes (spiny anteaters and platypuses). The presence of this region in the stomach of anteaters and many herbivores suggests that it serves as protection against physical damage. Eight mammalian orders include species with an enlarged stomach, which may be divided into permanent compartments, as seen in the rat, ox, and llama.

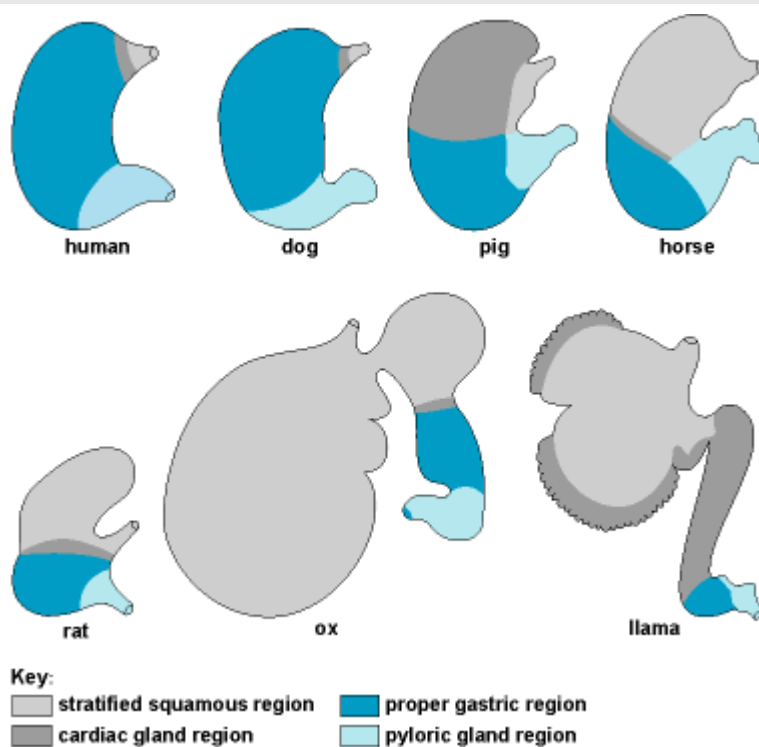
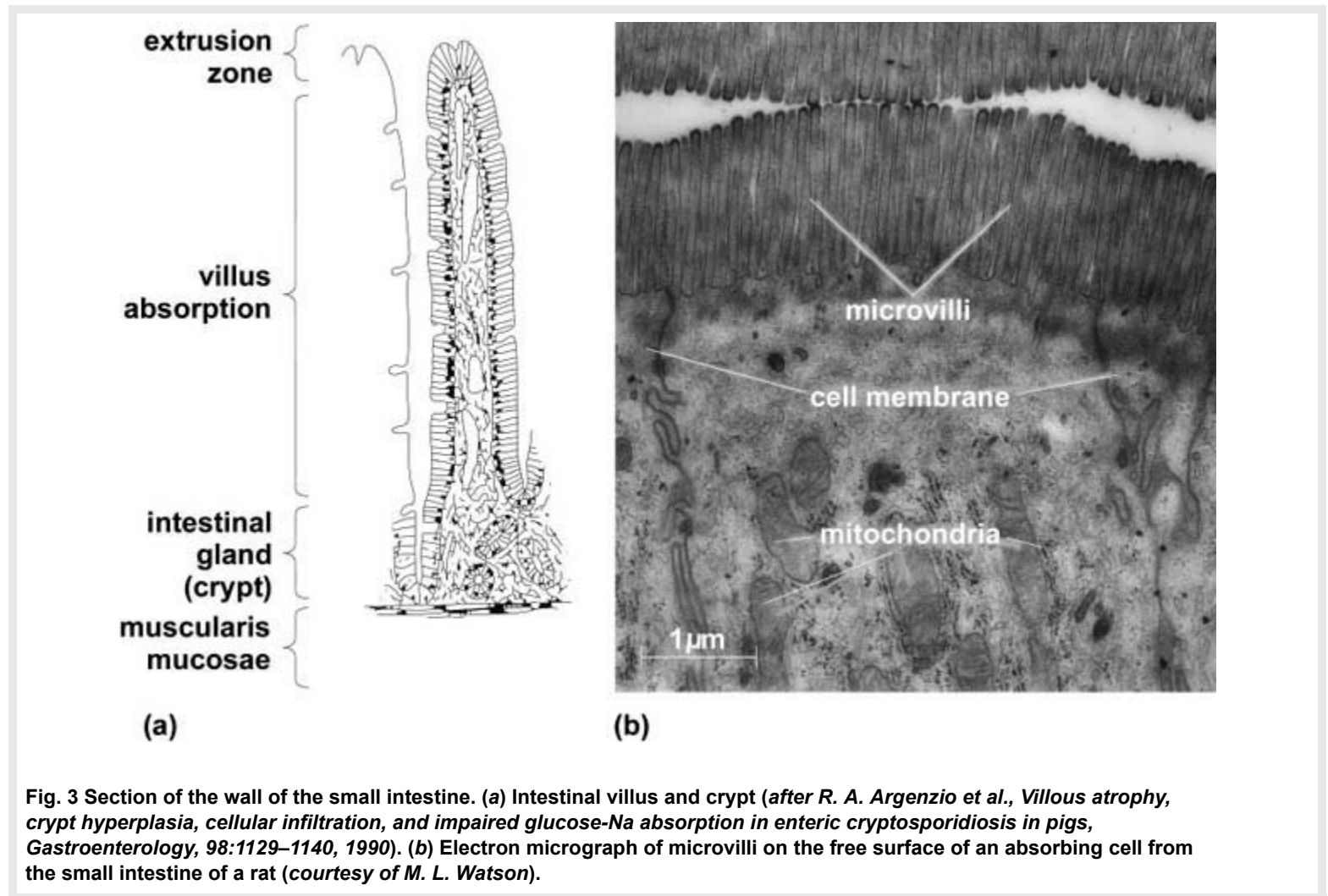


Fig. 2 Variations in the distribution of gastric epithelium and the degree of compartmentalization in the stomach of mammals. Stomachs are not drawn to the same scale; the stomach contents of the ox are approximately 70 times the volume and 14 times the weight of human stomach contents. (After C. E. Stevens and I. D. Hume, *Comparative Physiology of the Vertebrate Digestive System*, 2d ed., Cambridge University Press, 1995)

The midgut or small intestine is the principal site for the digestion of food and the absorption of nutrients. It is lined with a single layer of cells that secrete mucus and fluids, contain enzymes that aid in the final stages of carbohydrates and protein digestion, and absorb nutrients from the lumen into the circulatory system. The surface area of the lumen can be increased by a variety of means.

The lumen surface of the midgut of fish is increased by folds that form a spiral valve in some species and by 1–1000 pyloric ceca (blind sacs) in many other species ([Fig. 1](#)). In higher vertebrates the lumen surface is increased by the presence of villi, which are macroscopic projections of the epithelial and subepithelial tissue ([Fig. 3a](#)). A crypt at the base of each villus contains cells that secrete fluid into the gut and hormones that help regulate the functions of the digestive system. The crypts also contain cells that serve as precursors for the generation of absorptive and mucus-producing cells, which migrate up the villus surface and are eventually sloughed off into the lumen.



The lumen surface is also expanded by a brush border of microvilli on the lumen-facing (apical) surface of the midgut absorptive cells in all vertebrates ([Fig. 3b](#)). The brush border membranes contain enzymes that aid in the final digestion of food and mechanisms that provide for the selective absorption of nutrients. The luminal surface area of the human small intestine is increased 10-fold by the presence of villi and an additional 20-fold by the microvilli, resulting in a total surface area of 310,000 in.² (2,000,000 cm²), which is larger than a doubles tennis court.

Pancreas and biliary system

Digestion in the midgut is aided by secretions of digestive enzymes and fluid by pancreatic tissue, and secretion of bile by the liver. Pancreatic tissue is represented by primitive ceca along the midgut of cyclostomes and is distributed along the intestinal

wall, and even into the liver, of some species in the more advanced classes of fish. However, the pancreas is a compact organ in sharks, skates, rays, many teleosts, and all other vertebrates. See also: [Pancreas \(/content/pancreas/485000\)](#)

The liver is a compact organ in all vertebrates. One of its many functions is the secretion of bile. In most vertebrates, the bile is stored in the gallbladder and released into the intestine as needed, but a gallbladder is absent in some species of fish and mammals. Bile salts serve to emulsify lipids and increase their surface area available for digestion by the water-soluble lipase. See also: [Gallbladder \(/content/gallbladder/278000\)](#); [Liver \(/content/liver/387400\)](#)

Hindgut

The hindgut is the final site of digestion and absorption prior to defecation or evacuation of waste products. The hindgut of fish, amphibian larvae, and a few mammals is short and difficult to distinguish from the midgut by either its diameter or epithelial lining. However, the hindgut of adult amphibians and reptiles, birds, and most mammals is a distinct segment, which is separated from the midgut by a muscular sphincter or valve. It also tends to be larger in diameter. Thus, the midgut and hindgut of these animals are often referred to as the small intestine and the large intestine. See also: [Intestine \(/content/intestine/350300\)](#)

The hindgut of some reptiles and many mammals includes a blind sac or cecum near its junction with the midgut. A pair of ceca are present in the hindgut of many birds and a few mammalian species. The remainder of the hindgut consists of the colon and a short, straight, terminal segment, which is called the rectum in mammals. The digestive and urinary tracts exit separately from the body of most species of fish and mammals. However, in adult amphibians and the reptiles, birds, and some mammals, this segment terminates in a chamber called the cloaca, which also serves as an exit for the urinary and reproductive systems. The hindgut or, where present, the cloaca terminates in the anus. See also: [Colon \(/content/colon/149200\)](#); [Urinary system \(/content/urinary-system/724000\)](#)

The hindgut is similarly lined with a single layer of absorptive and mucus-secreting cells that originate in crypts. However, it lacks villi, and (with the exception of the cecum of birds) its absorptive cells lack digestive enzymes and the ability to absorb most nutrients. One major function of the hindgut is to reabsorb the fluids secreted into the upper digestive tract and (in animals that have a cloaca) excreted in the urine. It also serves as the principal site for the microbial production of nutrients in the herbivorous reptiles and birds and in most herbivorous mammals. Thus, the hindgut tends to be longest in animals that need to conserve water in an arid environment, and has a larger capacity in most herbivores.

Musculature

The digestion of food, absorption of nutrients, and excretion of waste products require the mixing of ingesta with digestive enzymes and the transit of ingesta and digesta through the digestive tract. The digestive tract of cyclostomes is enveloped with a single layer of muscle, and digesta transit is aided by cilia in the epithelial lining of the tract. However, in other vertebrates the contents are mixed and moved by an inner layer of circular muscle and an outer layer of muscle that runs longitudinally along the tract ([Fig. 4](#)).

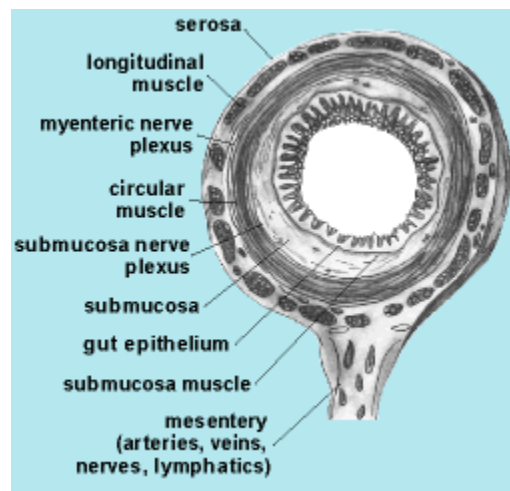


Fig. 4 Cross section of the layers of the gastrointestinal tract and the mesentery, which supplies it with blood vessels, lymphatic vessels, and nerves.

The initial act of deglutition and the final act by which waste products are defecated from the digestive tract are effected by striated muscle. This type of muscle is characterized by rapid contraction and is controlled by extrinsic nerves. The esophagus of fish and varying lengths of the mammalian esophagus are enveloped with striated muscle. However, the esophagus of amphibians, reptiles, and birds, and the entire gastrointestinal tract of all vertebrates are enveloped by smooth muscle. This smooth muscle contracts more slowly, and its rate of contraction is partly independent of external stimulation.

See also: [Muscle \(/content/muscle/439700\)](#)

Contraction of the circular muscles aids in the mixing and propulsion of digesta. At some sites along the digestive tract, the circular muscle is thicker and under almost continuous contraction, forming sphincters or valves that delay the movement of lumen contents in either direction. The anus has an additional sphincter, which is composed of striated muscle.

Contractions of the longitudinal muscles shorten the digestive tract. In the large intestine of some mammals and the stomach of a few, the longitudinal muscle is concentrated into three bands (taenia). Contraction of these longitudinal bands pulls these segments of the gut into a series of saccules. These saccules change their position along the gut with time and serve to both mix the contents and propel them through the gut.

Nerve and endocrine tissue

The initial act of deglutition and final act of defecation are under the voluntary control of the central nervous system. However, the remainder of the digestive system is subject to the involuntary control of nerves which release a variety of neurotransmitting or neuromodulating agents that either stimulate or inhibit muscular contractions and the secretions of glands and cells. The motor and secretory activities of the digestive system are also under the control of a wide range of other substances produced by endocrine cells that are released either distant from (hormones) or adjacent to (paracrine agents) their site of action. Although there are some major variations in the complement and activities of the neurotransmitters, neuromodulators, hormones, and paracrine agents, their basic patterns of control are similar.

Variations

The gastrointestinal tracts of adult amphibians and reptiles consist of a simple stomach, a midgut, and a hindgut that is generally expanded in diameter and referred to as the large intestine (**Fig. 5**). The hindgut is relatively short in adult amphibians, such as the toad, and in reptilian carnivores, such as the caiman. It tends to be longer in omnivorous reptiles, such as Blanding's turtle, and the proximal hindgut of most herbivorous reptiles, such as the green iguana, is expanded and

includes a cecum at its juncture with the midgut. The gastrointestinal tract of most birds includes a crop, proventriculus, gizzard, paired ceca, and a short straight section of hindgut that is generally referred to as the rectum. However, ceca are absent in some birds, small in others, such as the hawk, and more developed in omnivores, such as chickens. The largest ceca are found in most of the herbivores, such as grouse and rheas. The long colon of the herbivorous ostrich is unique among avian species.

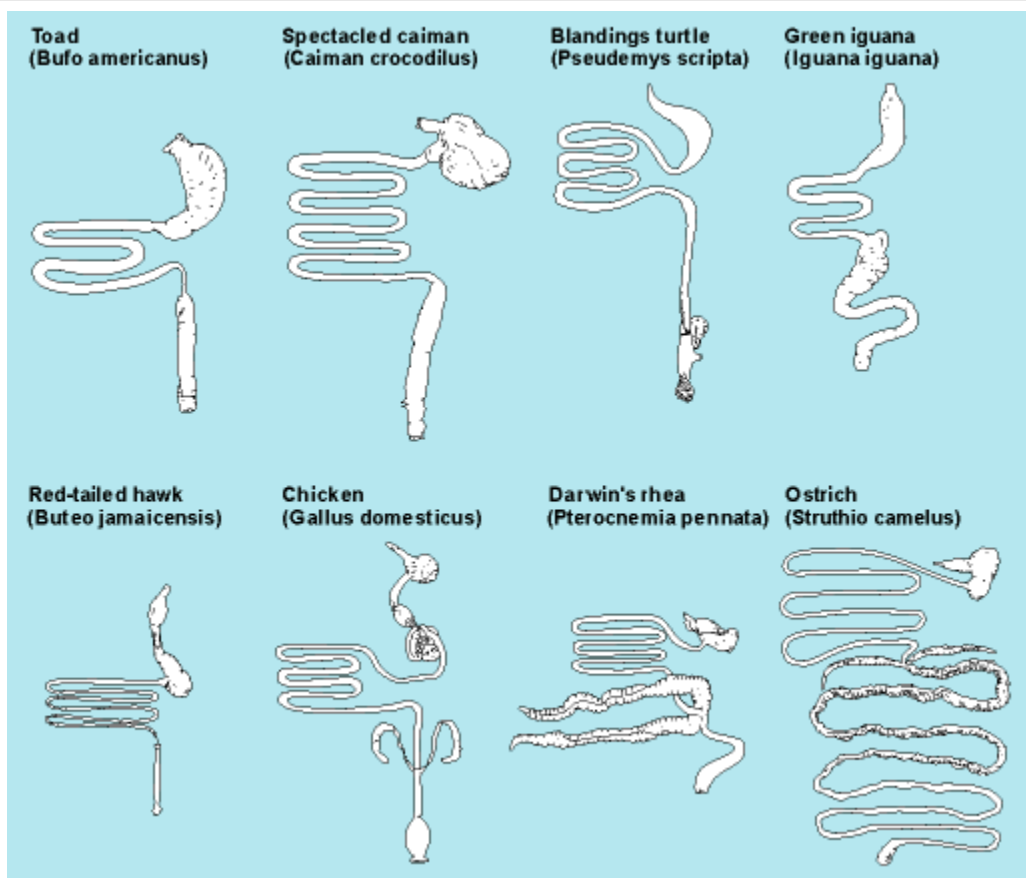


Fig. 5 Gastrointestinal tracts of amphibians, reptiles, and birds. (After C. E. Stevens and I. D. Hume, *Comparative Physiology of the Vertebrate Digestive System*, 2d ed., Cambridge University Press, 1995)

Mammals

The stomach and hindgut of mammals show an even wider range of structural variation (**Fig. 6**). Most mammals have a simple stomach, but the forestomach of many herbivorous mammals is large and divided into numerous compartments or saccules, as seen in the sheep and kangaroo. The same is true for other advanced ruminants (bovids, goats, antelope, deer, elk, giraffe), camelids, hippopotamuses, as well as the sloths, colobid monkeys, and cetaceans (dolphins, porpoise, and whales), hyrax, and some herbivorous rodents. Although present-day cetaceans feed on invertebrates, fish, or small mammals, the multicompartmental stomach is believed to have been inherited from herbivorous ancestors. The stomach is also expanded in blood-feeding vampire bats, reaching twice the body length of some species.

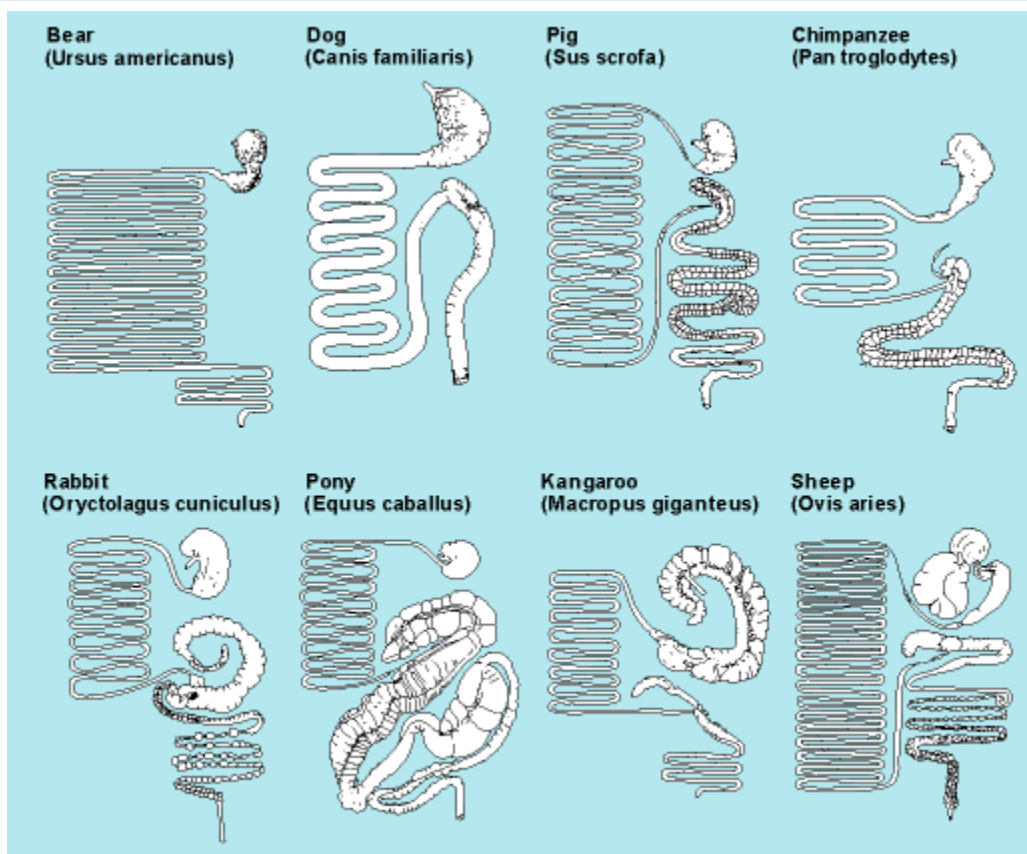


Fig. 6 Gastrointestinal tracts of carnivorous, omnivorous, and herbivorous mammals. (Bear and chimpanzee after C. E. Stevens and I. D. Hume, *Comparative Physiology of the Vertebrate Digestive System*, 2d ed., Cambridge University Press, 1995; pig after R. A. Argenzio and M. Southworth, *Sites of organic acid production and absorption in the gastrointestinal tract of the pig*, *Amer. J. Physiol.*, 118:454–460, 1974; dog, rabbit, pony, kangaroo, and sheep after C. E. Stevens, *Comparative physiology of the digestive system, in Dukes' Physiology of Domestic Animals*, ed. by M. J. Swenson, 9th ed., pp. 216–232, Cornell University Press).

The mammalian hindgut shows a similar range of variation. It is very short and indistinct in some insectivores, cetaceans, and the omnivorous bears, and relatively simple in most carnivores, such as the dog. The hindgut of omnivores tends to be more highly developed, and includes a sacculated cecum and colon in some omnivores, such as the chimpanzee and domesticated pig. The hindgut of mammalian herbivores with a simple stomach is dominated by either a large, sacculated cecum, as seen in the rabbit, or a large sacculated colon, such as that of the pony. However, regardless of diet, the hindgut tends to be short and simple in aquatic and semiaquatic species, such as cetaceans and hippos, and longest in desert species, such as camels.

Human

The anatomy of the human digestive system is similar to that of other mammalian omnivores (**Fig. 7**). The teeth and salivary glands are those of a mammalian omnivore, and the initial two-thirds of the esophagus is enveloped by striated muscle. A simple stomach is followed by an intestine, whose length consists of approximately two-thirds small bowel and one-third large bowel. The structures of the pancreas and biliary system show no major differences from those of other mammals. During early fetal development, a distinct, conical cecum is present and continues to grow until the sixth month of gestation. However, unlike other primates, the cecum recedes to become little more than a bulge in the proximal colon by the time of birth. The colon continues to lengthen after the birth and is sacculated throughout its length like that of the apes and a few monkeys but few other mammals.

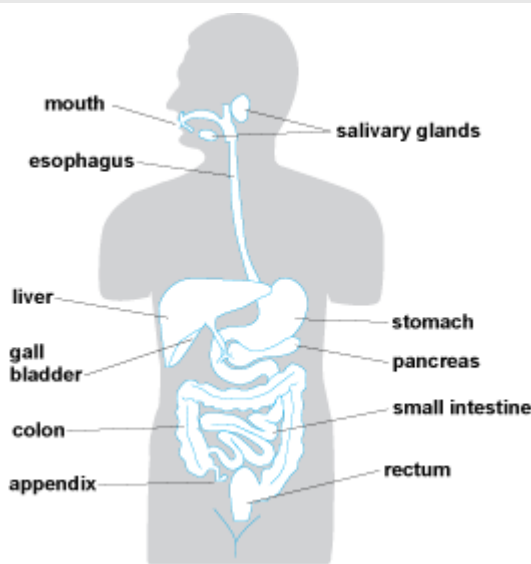


Fig. 7 Human digestive system. (After A. C. Guyton, *Textbook of Medical Physiology*, 8th ed., Saunders, 1991)

Physiology

The major physiological activities of the digestive system are motility, secretion, digestion, and absorption. Each activity can be affected by diet and, in the cold-blooded species, is reduced with a decrease in body temperature.

Motility

The mastication of food and the movement of ingesta and digesta through the digestive tract are controlled by the motor activity of muscular contractions. Pressure of food against the palate and back of the mouth stimulates a nerve reflex that passes through a deglutition center in the brain. This reflex closes the entrance into the respiratory system and stops respiration, to prevent the inspiration of food into the lungs, and initiates muscular contractions that pass food into the esophagus. The food (bolus) is then passed down the esophagus and into the stomach by a moving wave of muscular contractions (peristalsis) accompanied by inhibition of the esophageal sphincters.

The multicompartmental forestomach of ruminants undergoes a continuous series of complex, repetitive contractions that are controlled by the central nervous system. However, the gastric motility of most species and the intestinal motility of all vertebrates are controlled partially by the intrinsic characteristics of their smooth muscle cells. The result is production of either stationary (mixing) contractions of the stomach and intestine or a series of peristaltic contractions that carry digesta on through the tract.

Gastric peristalsis is initiated by cells in the middle of the stomach, which act as pacemakers for the contractions that travel over the distal half of the stomach. Pacemakers in the midgut and hindgut can also initiate waves of peristaltic contraction. However, pacemakers located near the cloaca of reptiles and birds or the midcolon of most mammals generate periodic waves of antiperistaltic contraction, which reflux digesta along the colon and into the cecum. These antiperistaltic waves increase the retention time needed for the absorption of electrolytes and water, and the multiplication of hindgut bacteria. Peristaltic and segmental contractions eventually move the digesta into the terminal hindgut, where it initiates the relaxation of sphincters and defecation.

Digestion

The diet of vertebrates contains carbohydrates, lipids, and protein, which provide the energy and building blocks for growth,

maintenance, and reproduction, and the vitamins that are required in small amounts for the regulation of metabolic processes. The lipids, proteins, and most of the carbohydrates require digestion for the release of nutrients that can be absorbed. Digestion is accomplished by enzymes produced by the digestive system (endogenous enzymes) or by bacteria that are normal residents of the digestive tract.

Dietary substrates

The carbohydrates consist of monosaccharides, disaccharides, and polysaccharides. The major monosaccharides in plants and animals are glucose or fructose, and the major disaccharides are the transport carbohydrates: sucrose (glucose-fructose), lactose (glucose-galactose), and trehalose (glucose-glucose). Sucrose is the principal transport carbohydrate in plants, trehalose is the blood sugar of insects, and lactose is the milk sugar of most mammals. Polysaccharides serve as either storage or structural carbohydrates. The main storage carbohydrates are the starches amylose and amylopectin in plants and glycogen in animals. The principal structural carbohydrates are the cellulose, hemicellulose, and pectin in the cell walls of plants, and chitin, which reinforces the exoskeleton cell walls of insects and many marine invertebrates. Starch and cellulose consist of long chains of glucose molecules. Hemicellulose, pectin, and chitin are made up of a variety of monosaccharides.

The major dietary lipids (fats and oils) are triglycerides and waxes that consist of esters of alcohols and fatty acids. Triglycerides are the major form of lipid storage in most animals and the seeds of plants. Wax esters constitute most of the lipids stored in many of the invertebrates in the food chain of marine fish and mammals. Protein consists of long chains of amino acids, arranged in various combinations and permutations that must be broken down to small peptides or amino acids for intestinal absorption. The cells of plants, animals, and bacteria also contain deoxyribonucleic acid (DNA), which provides genetic information, and ribonucleic acid (RNA), which controls the activities of the cells. The vitamins required by vertebrates consist of a group of fat-soluble (A, D, E, and K) and water-soluble (B-complex and C) organic compounds.

Endogenous enzymes

Plant and animal starches are converted to oligosaccharides (short-chain structures) and disaccharides by amylase, which is secreted by the salivary glands of some species and the pancreas of all vertebrates (see [table](#)). The end products of starch digestion, plus the dietary disaccharides, are converted to monosaccharides by enzymes in the brush border of the absorptive epithelial cells lining the small intestine. Chitin can be digested by the enzyme chitinase, which has been demonstrated in the gastric mucosa and pancreas of many mammals, birds, reptiles, and adult amphibians. However, vertebrates do not produce enzymes capable of digesting the structural polysaccharides of plants.

Table - Major dietary substrate end products and endogenous digestive enzymes*

Substrate	Extracellular enzymes	Intestinal mucosal enzymes	End products
Amylose	α Amylase	Maltase	Glucose
Amylopectin		Isomaltase	
Glycogen			
Chitin	Chitinase	Chitobiase	Glucosamine
Sucrose		Sucrase	Glucosamine
Lactose		Lactase	Glucose
			Galactose
Trehalose		Trehalase	Glucose

Triglycerides	Lipase		β -Monoglyceride
	Colipase		Fatty acids
Waxes	Lipase		Monohydric alcohol
	Esterase		Fatty acids
Protein	Pepsin	Aminopeptidase	Amino acids
	Trypsin	Tripeptidase	
	Chymotrypsin	Dipeptidase	
	Elastases		
	Carboxypeptidase A		
	Carboxypeptidase B		

*Modified from C. E. Stevens and I. D. Hume, *Comparative Physiology of the Vertebrate Digestive System*, 2d ed., Cambridge University Press, 1995.

Lipids are digested into alcohols, monoglycerides, and fatty acids by lipases and esterases, which are secreted predominantly by the pancreas. However, the lipases are water-soluble enzymes that can attack their substrate only at a lipid-water interface. Therefore, the lipids must be emulsified in order to provide the surface area required for efficient digestion. Emulsification is accomplished by the release of bile salts secreted by the liver and released into the midgut. The bile salts help form micelles, small spherical structures that contain the end products of lipid digestion and aid in their transfer to the lumen membrane of the epithelial cells for absorption into the cell. Once this process is complete, the bile salts are released and passed on to the distal midgut, where they are absorbed and circulated back to the liver.

Dietary protein is first broken down into long chains of amino acids (polypeptides) by gastric pepsin and pancreatic trypsin. The polypeptides are then attacked by other pancreatic proteases (chymotrypsin, carboxypeptidase, elastase) to form tripeptides, dipeptides, and amino acids. All of these enzymes are secreted in an inactive form to prevent the self-digestion of the secretory cells prior to their release. Pepsin is activated by the acidity resulting from the secretion of hydrochloric acid (HCl) into the stomach, and trypsin is activated by an enzyme (enterokinase) that is secreted by intestinal epithelium. The trypsin initially released by enterokinase activates the release of additional trypsin and the other pancreatic, proteolytic enzymes. Tri- and dipeptides are digested into amino acids by enzymes in the brush border and contents of midgut absorptive cells. Nucleic acids are digested by pancreatic ribonucleases into pentose sugars, purines, and pyrimidines.

Some vitamins must be released from their combination with other substances by digestive enzymes before they can be absorbed. Vitamin B₁₂, which is especially subject to destruction by digestive enzymes, is released from other compounds and combined with a substance called intrinsic factor secreted by the stomach. This combination protects it from digestion until it is released for absorption in the distal midgut. Therefore, a B₁₂ deficiency can result from dysfunctions of gastric secretion in humans.

The levels of various digestive enzymes tend to correlate with the levels of carbohydrate, lipid, and protein in the normal diet of a species. Herbivores and omnivores tend to produce higher levels of amylase, carnivores tend to produce higher levels of proteases, and the high concentrations of ribonucleases found in ruminants and kangaroos correlate with the high levels of microbial nucleic acid produced in their forestomach. The composition of digestive enzymes also varies with time in neonate mammals. All neonate mammals feed on milk, which is high in lipids and lactose in most species, and after weaning their diet that is usually low in fat and higher in other carbohydrates. The production of digestive enzymes adjusts to these changes in

the diet. For example, the newborn of most species produce high levels of lactase but low levels of the other carbohydrases. However, the latter appear well before weaning and reach their full complement at the time of birth, with a subsequent decrease in lactase production. These changes in enzyme composition anticipate the changes in diet and appear to be genetically programmed or “hard-wired” into the system. The levels of pancreatic amylase, lipase, and proteases (brush border enzymes) can also increase following an increase in the carbohydrate, lipid, or protein in the diet of adult animals.

Indigenous bacteria

Soon after birth or hatching the lumen surface and contents of the gastrointestinal tract become colonized by bacteria. Substantial numbers of bacteria can be found in all segments of the tract, but the highest numbers are present in those segments in which digesta are retained for prolonged periods of time at a relatively neutral pH. Bacteria are found in concentrations of 10^4 to 10^6 microorganisms per gram of fluid digesta in the midgut of fish and higher vertebrates. However, the development of the hindgut of terrestrial vertebrates into a major site of digesta retention was accompanied by its colonization with much higher numbers (10^{10} to 10^{11} per gram). In the ruminants and a few other species of mammalian herbivore, a large stomach serves as an additional site for colonization with similar numbers of bacteria.

Indigenous bacteria help protect the animal from pathogenic microorganisms by stimulating immunity and competing for substrates. They also convert dietary and endogenous substances that are not digested by endogenous enzymes into absorbable nutrients. Many species of indigenous bacteria can ferment sugars, starches, and structural carbohydrates into short-chain fatty acids. The short-chain fatty acids, which are predominantly acetic, propionic, and butyric acids, are readily absorbed and serve as an additional source of energy. These bacteria also synthesize microbial protein and the B-complex vitamins that may be useful to their host. See also: **[Bacterial physiology and metabolism \(/content/bacterial-physiology-and-metabolism/069000\)](#)**

The nutritional contributions of hindgut bacteria to mammals are illustrated in **Fig. 8**. Hindgut bacteria produce short-chain fatty acids by the fermentation of dietary carbohydrates that have escaped digestion and absorption in the midgut, and endogenous carbohydrate, such as that present in mucus. They also utilize dietary and endogenous compounds, such as digestive enzymes and urea, for the production of ammonia and microbial protein. Although most of the urea, which is the waste product of protein metabolism by the mammalian liver, is excreted by the kidneys, substantial amounts enter the gut by diffusion across its epithelial lining. The hindgut bacteria of birds, reptiles, and adult amphibians perform similar functions, except that uric acid is the waste product of hepatic protein metabolism and it enters the hindgut via the cloaca rather than by diffusion. The bacteria in the forestomach of mammalian herbivores also produce short-chain fatty acids from dietary carbohydrates, and ammonia and microbial protein from dietary protein and from urea, which reaches the forestomach via the saliva and diffusion across its epithelial lining.

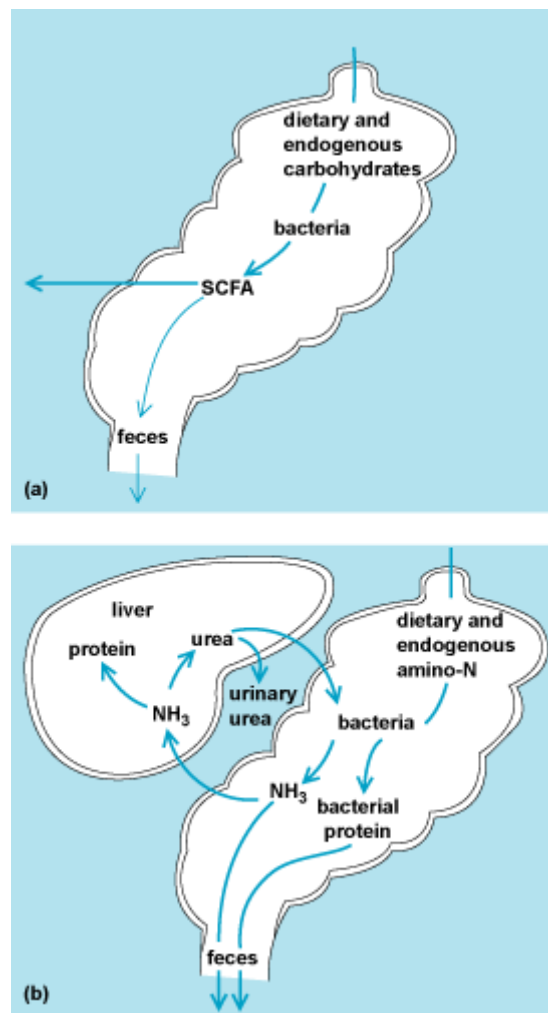


Fig. 8 Bacterial fermentation of carbohydrates and metabolism of nitrogenous compounds in the hindgut of mammals. (a) Fermentation of dietary and endogenous carbohydrates to short-chain fatty acids (SCFA), which are largely absorbed. (b) Bacterial production of ammonia and microbial protein from dietary and endogenous nitrogenous compounds. The endogenous compounds include digestive enzymes released in the upper digestive tract and the urea that passively diffuses into the gut. Ammonia is absorbed and returned to the liver for incorporation into protein and urea, which serves to conserve nitrogen and reduce the amounts of urea and water excreted by the kidneys. Bacteria in the hindgut of reptiles and birds serve similar functions, except that the uric acid that is produced instead of urea enters the hindgut via the cloaca. (Modified from A. M. Wrong and A. J. Vince, *Urea and ammonia metabolism in the human large intestine*, *Proc. Nutr. Soc.*, 43:77–86, 1984)

Absorption of short-chain fatty acids provides the major source of the energy required by hindgut and forestomach epithelial cells and a portion of the maintenance energy required by the species. Some of the ammonia is used for the synthesis of bacterial protein, but most of the remainder is absorbed and returned to the liver for the synthesis of protein and urea. This aids in the conservation of nitrogen and reduces the amount of urea (and water) that must be excreted in the urine. The absorption of short-chain fatty acids and ammonia also plays a critical role in the hindgut absorption of water. The microbial protein and B-complex vitamins synthesized by these bacteria also can be utilized as nutrients by coprophagic and forestomach fermenting species.

The contributions of indigenous bacteria to the production and conservation of nutrients are greatest in herbivores. Although it has been estimated that short-chain fatty acid absorption provides 4% of total maintenance energy requirement by dogs and 6–10% of the maintenance energy required by humans, they can account for 30% of the maintenance energy of rabbits and up to 70% of maintenance energy of horses and ruminants. The dietary protein and water requirements of rabbits, horses, and ruminants can be greatly reduced by the recycling of urea nitrogen; and the dietary requirements for both protein and B-vitamins are substantially reduced by coprophagy in rabbits and foregut fermentation in ruminants.

Herbivores

The appearance of herbivores that could subsist largely on the leaves, petioles, and stems of plants played a significant role in the expansion and distribution of vertebrates. Herbivory requires the ingestion of large quantities of plant material, its reduction to small particle size, and either the rapid passage of this material through the gut or its prolonged storage for bacterial fermentation. Herbivores are relatively rare among fish, larval amphibians, reptiles, and birds, and all adult amphibians are carnivores. Most herbivorous fish reduce plant material to particle size by the use of a pharyngeal mill or gizzardlike stomach and pass it rapidly through the intestine, using their midgut as the principal site of microbial fermentation. The midgut is also the principal site in larval amphibians and the Florida red-bellied turtle, emu, and panda, but the colon is the principal site in most herbivorous reptiles.

The rarity of herbivorous reptiles has been attributed to the lack of an efficient masticatory apparatus and small body size of most reptiles. The articulation of the reptilian jaws precludes the grinding action that can reduce plant material to a fine size, and the increase in mass-specific metabolic rate with a decrease in body mass limits the gut capacity and, thus, minimum body size of most reptilian herbivores to about 300 g (11 oz). This rarity of herbivores among present-day reptiles has raised questions about why herbivory was so successful for dinosaurs. The sauropods included many herbivores and the largest species of dinosaurs, and all ornithopods are believed to have been herbivores. Their success has been attributed partly to a gizzardlike stomach in the sauropods and an efficient masticatory apparatus in the ornithopods. It has also been attributed to the possibility that many dinosaurs were endothermic. However, studies of present-day reptiles suggest that the lower rates of metabolism and digesta passage that accompany a reduction in the ambient temperature may compensate for the reduction in the rates of digestion and absorption. Therefore, the rarity of present-day herbivores may be due to lack of an efficient masticatory apparatus and the susceptibility of larger species to predation by endotherms.

Although the gizzard of birds provides an efficient apparatus for the grinding of plant material, their gut capacity is limited by the requirement for flight. The herbivorous birds are confined to grouse, partridge, and the hoatzin, which fly only short distances, and the flightless rheas, emus, and ostriches. The midgut is the main site of microbial fermentation in the emu, and the colon is the principal site in the ostrich. However, among the smaller herbivores, the ceca are the principal sites in the rhea, grouse, and partridge, and the foregut (crop and distal esophagus) is the principal site in the hoatzin. The cecal fermenters include snow partridge and snow cocks, which inhabit altitudes 5000 m (16,400 ft) above sea level, and the arctic ptarmigan.

In contrast to the fish, amphibians, reptiles, and birds, herbivory was adopted by a high percentage of mammals. Herbivorous species are found in 11 of the 20 mammalian orders, and 5 of these orders contain only herbivores. The herbivorous mammals constitute the largest number of species, include the largest terrestrial species, show the widest range of ecological distribution, and provide over 90% of the mammalian biomass. Their success is due to an efficient masticatory apparatus and the development of a hindgut or foregut that can store large amounts of plant material for long periods of time.

The principal site of microbial fermentation in the herbivorous panda is a long midgut, similar to that of the bear ([Fig. 6](#)), but other mammalian herbivores have adopted the strategies of colon, cecal, or foregut fermentation. Many herbivores over 30 kg (66 lb) in body weight, including the wombats, orangutans, gorillas, tapirs, equids, rhinos, and elephants, have adopted the colon as principal site of microbial fermentation. However, most herbivores less than 30 kg in body weight are cecal fermenters, and most herbivores of intermediate body weight are foregut fermenters.

As with the birds, most small mammalian herbivores overcame the limitations of body weight on gut capacity by the rapid passage of large digesta particles through the gut and selective retention of fluid, bacteria, and small particles in an enlarged cecum. Included are the lagomorphs (rabbits, hares, and pica), folivorous marsupials (koalas, greater gliders, cuscuses, and some possums), and the herbivorous rodents. Many of these species practice coprophagy, which recovers microbial protein

and B-vitamins from the feces; and some of these species ingest only the nutritionally rich feces that are derived from a periodic release of cecal contents. Lagomorphs and herbivorous rodents are distributed throughout all regions of the world. The forestomach is the principal site of microbial fermentation in a few small herbivores (rat kangaroos, sloths, colobid monkeys, and the smallest ruminants) and most intermediate-sized herbivores (kangaroos, wallabies, camelids, and advanced ruminants).

Colon and cecal fermenters have the advantages of recovering nutrients from the readily digestible components of the diet from their midgut, prior to the less efficient process of microbial digestion, and increasing their food intake, digesta passage, and recovery of these nutrients on high-fiber diets. However, foregut and coprophagic cecal fermenters make use of the protein and B-vitamins synthesized by gut microbes. Foregut fermentation sacrifices the advantage of recovering readily available nutrients prior to microbial fermentation. However, it allows the microbial digestion of plant toxins and provides the most efficient system for the recovery of large amounts of the electrolytes and water secreted by herbivores.

Ruminants have the additional ability of selectively retaining large particles of plant fiber in their forestomach. This retention allows a more complete fermentation of low-quality forage and accounts for the ruminants' adaptation to desert, high altitudes, and the arctic tundra. Therefore, the adoption of cecal and foregut fermentation expanded herbivory into smaller birds and mammals, and extended their distribution into regions where forage and water are sparse.

Absorption

The cells lining the small intestine of many newborn mammals are capable of absorbing intestinal contents by a process called phagocytosis. Intestinal contents are engulfed by the lumen-facing membrane into cell vesicles. Cellular enzymes digest most of the vesicular contents, but the immunoglobulins in the mother's milk are transported intact and provide the newborn with a passive immunity to many diseases. Phagocytosis is absent in the newborn of some species and short-termed in others, such as humans. Although it can continue for longer periods in a few species, such as the rat, it disappears in all mammals by the time of weaning.

The epithelial cells that line the gastrointestinal tract are closely attached to one another at their lumen-facing border by tight junctions, which are relatively impermeable to most substances other than water. Therefore, the major restriction for the absorption of most substances from the lumen into the blood is the apical and basolateral membranes of these cells. The epithelial cell membranes consist of a lipid-protein barrier that is permeated with a limited number of small, water-filled pores. Thus, they are relatively permeable to lipid-soluble substances and water but relatively impermeable to the passive diffusion of most water-soluble substances.

Lipid-soluble substances

Lipid-soluble substances can be transported across the apical cell membranes by passive diffusion down their concentration gradient. The short- and medium-chain fatty acids that result from lipid digestion in the small intestine pass directly into the blood. However, the monoglycerides and long-chain fatty acids are resynthesized into triglycerides by the epithelial cells in the midgut and incorporated into small spheres (chylomicrons), which are transported across the basolateral membrane into the lymphatic system. Fat-soluble vitamins, long-chain alcohols, and other lipids also appear to be incorporated into chylomicrons and to enter the lymphatic system.

Water-soluble compounds

The intestinal cell membranes are relatively impermeable to the passive diffusion of water-soluble monosaccharides, amino acids, vitamins, and minerals that constitute a major portion of the required nutrients. These nutrients are selectively transferred across the intestinal cell membranes by carrier-mediated transport. Membrane carriers combine with the nutrient

at one membrane surface and pass it across the membrane for release at the opposing surface. Some simply facilitate the diffusion of a substance down its concentration gradient; others are capable of transporting a nutrient against its concentration gradient, which requires either a direct or indirect investment of cellular energy. See also: **Cell membranes (/content/cell-membranes/116500)**

Fructose is transported by a carrier-mediated process that facilitates its diffusion across the apical membrane, but glucose and galactose are transported into the epithelial cells of the small intestine against their respective concentration gradients. Their absorption into the cell is dependent upon the simultaneous absorption of sodium ions (Na^+) down the concentration gradient provided by transport of sodium by another carrier against its concentration gradient across the basolateral membrane. This relationship between glucose and sodium absorption was first suggested by the finding that cola beverages, which contain high levels of glucose and sodium, were much more effective than glucose solutions when administered orally for treatment of the diarrhea associated with cholera. The amino acids, dipeptides, and B-complex vitamins also are transported across the apical membrane of these intestinal cells by a variety of Na^+ -dependent, carrier-mediated transport systems. The transport of these substances across the basolateral membranes of the cell is accomplished by sodium-independent carriers.

Short-chain fatty acids and ammonia

The short-chain fatty acids and ammonia derived from bacterial fermentation are present in both undissociated and dissociated (ionized) form. Cell membranes are relatively permeable to the passive diffusion of the lipid soluble undissociated short-chain fatty acids and ammonia, but impermeable to the diffusion of the water-soluble ionized forms that predominate at the normal pH of hindgut and forestomach contents. Therefore, a reduction in digesta pH tends to increase the rate of short-chain fatty acid absorption and decrease the rate of ammonia absorption. However, there is also evidence for the absorption of short-chain fatty acid ions in exchange for bicarbonate (HCO_3^-) and ammonia ions (NH_4^+) in exchange for hydrogen (H^+).

Minerals

The metabolic processes of the body require a number of different minerals. Some such as iron, calcium, sodium, and chloride are required in relatively large quantities. Others such as manganese and zinc are labeled trace minerals because they are required in only minute amounts. The absorption of iron and calcium involves membrane carriers. Absorption of sodium and chloride ions is discussed below.

Diet adaptations

The rates of nutrient absorption can be affected by the diet. The ratio of sugar to amino acid absorption appears to be highest in the herbivores and lowest in the carnivores of all classes of vertebrates. A change from a high-carbohydrate and low-protein diet to a high-protein and low-carbohydrate diet also can increase the rate of glucose absorption and decrease the rate of amino acid absorption by individual animals. An increase in dietary calcium, iron, copper, phosphorus, or B-complex vitamins, which can be toxic at high concentrations, appears to decrease their rates of absorption.

Electrolytes and water

The nutrient that is required in largest quantity for digestion, absorption, metabolism, and excretion of waste products is water. Because it readily diffuses across cell membranes down its concentration gradient, the net secretion or absorption of water is determined by the net secretion or absorption of all other substances. Sodium, chloride, and bicarbonate are the principal ions that are present in the extracellular fluids that bathe the body cells of all vertebrates and that are transported across cell membranes. Therefore, the transport of these electrolytes is the major driving force for the secretion or absorption of water.

Secretion

Solubilization, digestion, and the transit of food and digesta by the alimentary tract require the secretion of large volumes of fluid. Secretions by the salivary glands, pancreas, biliary system, and intestinal cells contain high concentrations of sodium, chloride, and bicarbonate ions, and gastric secretions contain high levels of hydrogen and chloride ions. The secretion of hydrochloric acid reduces the pH of gastric contents to the levels required for activation and activity of pepsin. However, the midgut requires a more alkaline pH for protection of its epithelium and the activation of the pancreatic enzymes. This is accomplished by the bicarbonate ions secreted by the pancreas, biliary system, and intestinal mucosa. The short-chain fatty acids produced by microbial fermentation can also reduce the pH of gut contents, with damaging results. Short-chain fatty acids produced in the forestomach are neutralized by bicarbonate secreted from the salivary glands and the forestomach epithelium, and those produced in the hindgut are neutralized by the bicarbonate secreted into the midgut and hindgut. See *also*: [**pH regulation \(biology\) \(/content/ph-regulation-biology/504050\)**](#)

Under normal conditions, an adult human consumes 2 liters (1.8 qt) of water per day, and the digestive system secretes an additional 7 liters (6.4 qt) of fluid per day; resulting in a total of 9 liters (8.2 qt) of fluid. This is equivalent to 40% of the water in the extracellular fluid space. An uncompensated loss of 15% of the extracellular fluid volume can produce clinical signs of dehydration, and a loss of 35% can result in death. This is prevented by absorption of 7 liters of this fluid by the small intestine and an additional 1.4 liters (1.3 qt) by the large intestine, leaving only 0.1 liter (0.09 qt) for excretion into the feces. Although the large intestine normally absorbs only 20% of this fluid, this percentage is critical, and its absorptive capacity can be doubled if necessary. The daily secretions of the digestive system are much higher in herbivores, reaching levels equivalent to two or three times the extracellular fluid in the sheep and horse, but with a similar 95–98% recovery prior to excretion.

Absorption

The absorption of water from the midgut is accomplished mainly by the absorption of sodium, chloride, vitamins, and the end products of carbohydrate, lipid, and protein digestion by the endogenous enzymes. Some of the sodium is absorbed in conjunction with monosaccharide, amino acid, and vitamin absorption, but some of the sodium and most of the chloride are absorbed by a mechanism that exchanges sodium for the hydrogen and chloride for the bicarbonate in the epithelial cells. The hydrogen and bicarbonate entering the gut combine to form carbon dioxide (CO₂) and water.

The hindgut appears to have evolved initially for conservation of the electrolytes, water, and nitrogen in both the digestive secretions and urinary excretions of terrestrial vertebrates. The kidney is the principal organ for excretion of metabolic waste products, which it accomplishes by continuously filtering blood through the glomerulus of the nephron and reabsorbing water and nutrients from the renal tubule. The earliest vertebrates are believed to have been freshwater fish, whose major problem was the rejection or elimination of excess water. Freshwater fish do not intentionally drink water, and excess water is excreted by the kidneys.

Marine fish face the opposite problem: the potential loss of water and gain in sodium chloride (NaCl) due to the high salinity and osmotic activity of sea- water. Although marine fish drink seawater, its osmotic effect on the digestive system is reduced by the absorption of sodium chloride from their esophagus. Hagfish, sharks, and rays have resolved the osmotic problem by having body fluids that are isotonic or hypertonic to seawater. However, this problem is resolved in most marine fish by the absence of glomerular filtration by the kidney and active secretion of sodium chloride by the gills and other tissues such as the rectal glands of sharks. See *also*: [**Kidney \(/content/kidney/364000\)**](#)

Terrestrial animals must conserve both their water and electrolytes against loss to the environment. Their kidneys, like those of freshwater fish, filter blood and reabsorb electrolytes and water, but the urine of amphibians, reptiles, and birds is excreted

into a cloaca. Antiperistaltic contractions then reflux urine along the length of the hindgut of many reptiles and birds, allowing the cloaca and hindgut to aid the kidney in the recovery of electrolytes and water from both the digestive secretions and urinary excretions.

In most mammals, the digestive and urinary systems exit the body separately, and the nephron of the kidney is lengthened by the loop of Henle, which provides for more efficient recovery of water. The hindgut continues to function as the final site for recovery of digestive fluids, and tends to be longer than that of lower vertebrates and longest in those that inhabit arid environments. Pacemaker tissue located in the midcolon generates antiperistaltic waves of contraction, which continue to aid retention of digesta in the cecum and proximal colon.

The absorption of water from the hindgut is due principally to the absorption of sodium, short-chain fatty acids, and ammonia. Sodium is absorbed in exchange for hydrogen by a mechanism that partly depends on short-chain fatty acid absorption and by a mechanism that transports sodium alone. Thus, prolonged retention of digesta by the hindgut of terrestrial vertebrates increased both the time available for absorption of electrolytes and water, and the multiplication of endogenous bacteria that contribute to this process.

Neural and endocrine control

The motor and secretory activities of the digestive system are controlled and integrated by the nervous system, hormones, and paracrine secretions. Many of these activities are controlled by nerve reflexes, consisting of sensory neurons with receptors in the digestive tract that pass information, via other neurons in the central nervous system and gut wall, back to the digestive tract. The latter neurons release neurotransmitters or modulators that stimulate or inhibit muscular contraction or cellular secretions. Reflexes responsible for the initial stage of deglutition and final stage of defecation are monitored through brain centers, allowing for voluntary control of these activities. However, most of the motor and secretory events in the digestive system are under the involuntary and sometimes interactive control of a large number of neurotransmitters, neuromodulators, hormones, and paracrine agents.

Although much of the neuroendocrine control provides a direct response to conditions in a given segment of the gut, some of these responses prepare a following segment for what is to come, or tune down the activities in a previous segment. The sight or smell of food can stimulate gastric secretions, and the act of deglutition produces a receptive relaxation of the stomach. Distention of the stomach can stimulate contractions of the colon, which accounts for the relationship between meals and defecation. Similarly, the entrance of partially digested food into the small intestine not only stimulates the secretion of pancreatic fluid and the release of bile but also decreases the rates of gastric secretion and motility.

For example, the sight or smell of food and its presence in the stomach result in neural and chemical stimulation of the release of the hormone gastrin from the stomach wall. Gastrin stimulates the secretion of hydrochloric acid and pepsinogen for the digestion of protein. As the digestive process progresses, the passage of hydrochloric acid and the end products of gastric digestion into the small intestine stimulates the release of the hormones secretin and cholecystokinin from the intestinal wall. These hormones act to inhibit the secretion of gastrin and stimulate the release of fluid and enzymes from the pancreas and the release of bile from the gallbladder. The high concentration of bicarbonate ions in these secretions neutralizes the hydrochloric acid in the gastric effluent, and the pancreatic enzymes and bile aid in the digestion of starch, proteins, and lipids.

Adaptations

Some characteristics of the vertebrate digestive system are common to all classes of vertebrates and appear to have been conserved in their evolution. Included are most of the enzymes responsible for digestion of carbohydrates, proteins, and

lipids, and the mechanisms for absorption of nutrients by the midgut or small intestine. However, the headgut and hindgut show a variety of adaptations to the diet, the environment, or physiological characteristics of the animal.

Many adaptations of the mouthparts and feeding practices to the diet are seen among species in all classes of vertebrates. Prolonged retention of digesta by the hindgut or large intestine for the recovery of urinary and digestive fluids appears to have first developed in the adult amphibians. This resulted in the production of large populations of indigenous bacteria, whose digestive end products aid in the resorption of fluids and can provide additional nutrients. Further adaptations of the hindgut led to the evolution of herbivores, which have access to a much wider range of food. The major advances in the digestive system of mammals were the development of an extremely efficient masticatory apparatus and, in some species, a more complex and voluminous large intestine or stomach. These advances account for the marked success of the mammalian herbivores and suggest that the success of the herbivorous dinosaurs may have been based on similar developments.

The digestive systems of different species are designed for different diets. The digestive system of most carnivores is designed for the intermittent consumption of high-protein diets, often at intervals of 12–18 h in many mammalian carnivores and longer periods of time for cold-blooded species. The herbivore digestive system is designed for the almost continuous consumption of large volumes of plant material. When left to their normal diet, horses and elephants may spend 18 h a day foraging for food, and ruminants spend 8 h grazing and an additional 8 h remasticating their cud.

A number of the digestive diseases of herbivores can be attributed to the feeding of high-concentrate, low-fiber diets. High levels of rapidly fermentable starch can result in a fulminating production of short-chain fatty acids and the gases CO₂ and methane (CH₄) in the forestomach of cattle and the large intestine of horses. The short-chain fatty acids lower the pH of gut contents, resulting in the growth of lactobacilli and the production of lactic acid. The high levels of short-chain and lactic acids can produce a hypertonic digesta and systemic dehydration, and their absorption can damage the gut epithelium, inhibit gut motility, and result in systemic acidosis. Excessive gas production can distend and displace the gut and inhibit its motility. This syndrome is responsible for a number of diseases involving the forestomach of ruminants and for the high incidence of torsion, impaction, and colic in the large intestine of horses on high-concentrate diets. Although humans are omnivores, the much greater prevalence of cancer and other diseases of the colon on the high-protein, high-carbohydrate, high-lipid, low-fiber diets of affluent Western societies suggests that the human large intestine is subject to similar problems.

The nutritional requirements of vertebrates are provided by an extremely complex system with a variety of different and often exotic adaptations to the diet, habitat, and other physiological characteristics of a species. Studies of these adaptations have provided important contributions to understanding of basic physiological mechanisms. They also provide information needed for the maintenance of domesticated and captive (zoo) animals and survival of endangered species. The extinction of vertebrates at a rate of approximately one species each year could be prevented or at least delayed by a better understanding of these species and their contributions to the beauty and balance of nature.

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