Figure 41.2 Before and after gastric bypass surgery.

factor? In one study, the surgery reduced ghrelin levels by 77 percent. Researchers are working to develop a drug that can slow the body's synthesis or release of this hormone, which might be a less risky alternative to surgery.

At the other end of the spectrum are individuals who cannot gain enough weight. For instance, appetite tends to decline with age. Among some of the elderly, appetite loss is severe enough to endanger health. **Cholecystokinin** (CCK) may promote appetite suppression. A new drug that blocks this hormone's secretion may help keep the elderly from being malnourished. Conversely, a drug that induces its secretion might help prevent obesity.

Questions about food intake and body weight lead us into the world of **nutrition**. The word encompasses all the processes by which an animal ingests and digests food, then absorbs the released nutrients as energy sources and building blocks for cells. When all works well, inputs balance the outputs, and weight remains within a range that promotes good health.

How Would You Vote?

Many nutritionists suspect that increasing consumption of "fast foods" is contributing to rising levels of obesity. Should fast-food labels carry consumer warnings, as alcohol and cigarette labels do? See BiologyNow for details, then vote online.

Key Concepts

OVERVIEW OF DIGESTIVE SYSTEMS

A digestive system is saclike or a tube through the body with openings at both ends. Those of complex animals interact with circulatory, respiratory, and urinary systems to supply the body with food and water, dispose of residues and wastes, and help maintain the internal environment. Section 41.1

HUMAN DIGESTIVE SYSTEM

The human digestive system is functionally divided into regions of mechanical breakdown, chemical breakdown, absorption, storage, and elimination. Accessory organs assist in these functions. Sections 41.2–41.6

ORGANIC METABOLISM AND NUTRITION

The body converts nutrients absorbed from the gut to its own complex carbohydrates, lipids, proteins, and nucleic acids. Complex carbohydrates are the main source of dietary glucose. An ideal diet provides all the necessary nutrients, vitamins, and minerals to support metabolism. Sections 41.7–41.9

BALANCING CALORIC INPUTS AND OUTPUTS

Suitable body weight and overall health are maintained when caloric intake balances caloric output—mainly metabolism and physical activity. Section 41.10

Links to Earlier Concepts

This chapter expands on the sampling of digestive systems in the survey of animal diversity (Chapters 25, 26). You will again consider complex carbohydrates, lipids, and proteins (Sections 3.3–3.5) and the nature of organic metabolism, especially the disposition of glucose (8.6, 36.6). You will draw on your knowledge of diffusion, transport mechanisms, and osmosis (5.3–5.5). You may wish to review the introduction to pH and buffer systems (2.6).

41.1 The Nature of Digestive Systems

LINKS TO SECTIONS 25..2, 26.10

Every animal ingests and digests food, then absorbs and converts the released nutrients to the body's carbohydrates, lipids, proteins, and nucleic acids. Let's now build on the examples given in Chapters 25 and 26.

A **digestive system** functions in nutritional processes. This body cavity or tube mechanically and chemically reduces food to small particles, and then to molecules that are small enough for absorption into the internal environment. The system also eliminates unabsorbed residues. By interacting with other systems, especially those shown in Figure 41.3*a*, a digestive system also helps maintain homeostasis for the body as a whole. As you will see, these direct and indirect interactions are under neural and hormonal control.

INCOMPLETE AND COMPLETE SYSTEMS

Recall, from Section 25.2, that some invertebrates have an *incomplete* digestive system. Food enters and wastes leave their saclike gut through a single opening at the body surface. For flatworms, a saclike, branching gut cavity opens at the start of a pharynx, a muscular tube (Figure 41.3*b*). Food enters the sac, is partly digested, and circulates to cells even as wastes are sent out. This two-way traffic does not favor regional specialization.

Most animals have a *complete* digestive system—a tube that has a mouth (an opening at one end for food intake) and an anus (an opening at the other end for eliminating unabsorbed residues). The tube is divided into specialized food processing and storage regions.

Figure 41.3*c* shows the complete digestive system of a frog. Between the mouth and anus are a stomach, large and small intestines, and other organs. The liver, gallbladder, and pancreas are all organs with accessory roles. They secrete enzymes or other products into the small intestine. The complete digestive system of birds also has specialized regions (Figure 41.3*d*).

Regardless of its complexity, a complete digestive system carries out five overall tasks:

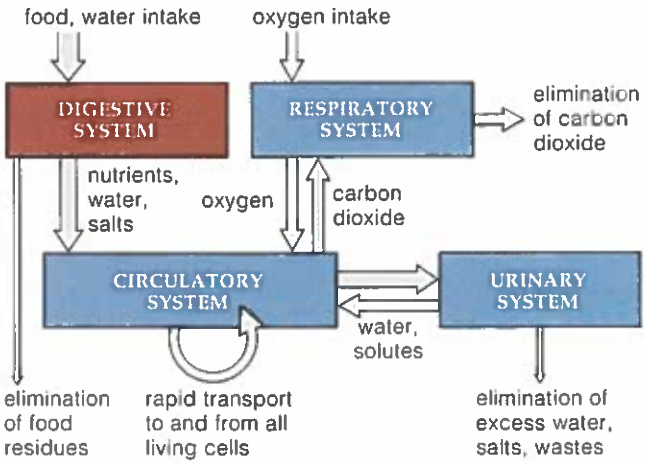
1. *Mechanical processing and motility.* Movements that break up, mix, and directionally propel food material.

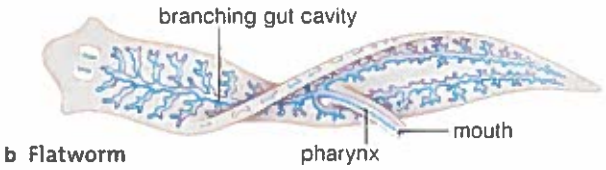
2. *Secretion.* Release of substances, especially digestive enzymes, into the *lumen*—the space inside the tube.

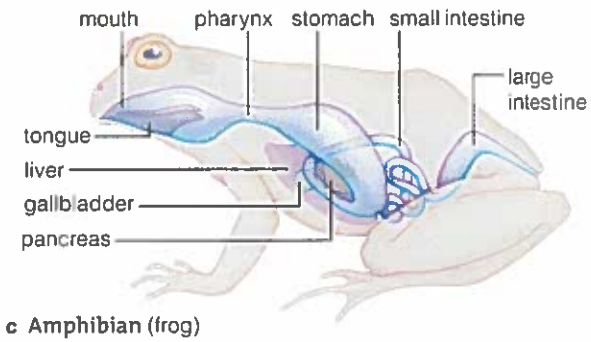
3. *Digestion.* Breakdown of food to particles, then to nutrient molecules small enough to be absorbed.

4. *Absorption.* Uptake of digested nutrients and water across the tube wall, into extracellular fluid.

5. *Elimination.* Expulsion, from the end of the gut, of undigested and unabsorbed residues.







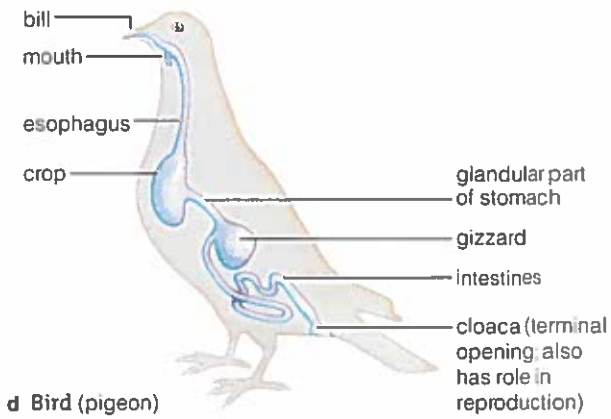
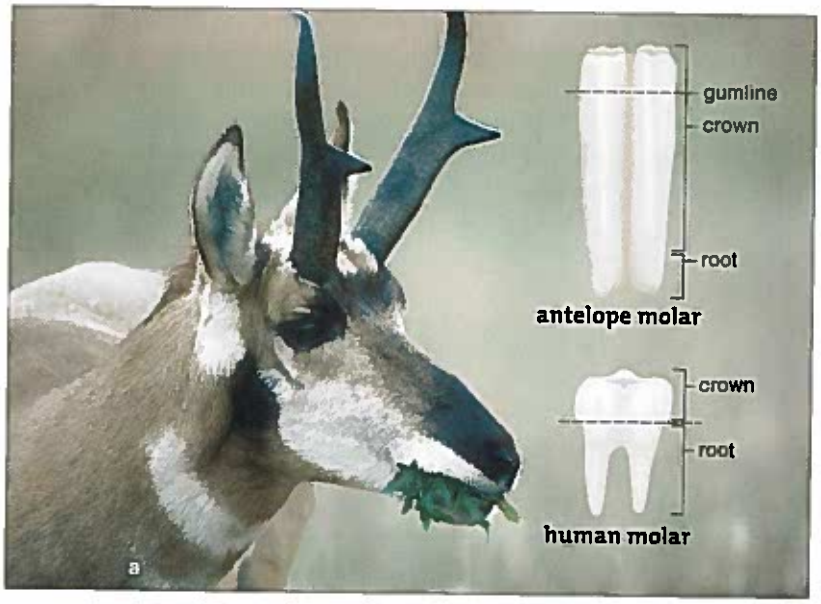


Figure 41.3 ***Animated!*** (**a**) Organ systems with roles in the uptake, processing, and distribution of nutrients and water in complex animals. Comparison of an incomplete digestive system (**b**) with two complete digestive systems (**c**,**d**).



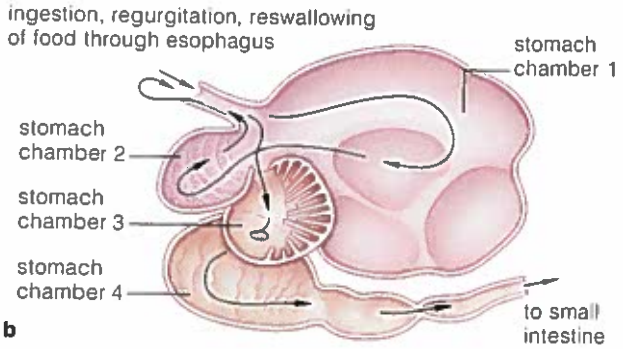


Figure 41.4 ***Animated!*** (**a**) Molars of a pronghorn antelope (*Antiloca, americana*) and a human. (**b**) Multiple chambers of an antelope stomach. In the first two chambers, food becomes mixed with fluid and is exposed fermentation by microbial symbionts. Some symbionts degrade cellulose others synthesize organic compounds, fatty acids, and vitamins. The ho uses part of these substances. Partially digested food is regurgitated int the mouth, chewed, and then swallowed. It enters the third chamber and is digested again before entering the last stomach chamber.

CORRELATIONS WITH FEEDING BEHAVIOR

You can correlate any digestive system's specialized regions with feeding behavior. Consider a pigeon. Its *food-intake* region includes a bill that pecks at seeds on the ground. Its *food-processing* region, a tube compactly centered in the body mass, balances the bird when it flies. As in other seed-eating birds, a *crop* bulges out from the tube between the mouth and the gut. This stretchable sac lets a pigeon eat fast. An eat-and-run strategy reduces the time the bird must spend on the ground, when it is most vulnerable to predators.

Part of the pigeon stomach, a *gizzard*, is lined with hard protein particles that can smash and crush food. As in other birds, the length of time it takes to process its preferred type of food correlates with the length of the intestines. Birds that eat mainly hard seeds have longer intestines than birds that eat insects, fruit, and nectar. In all birds, waste products of digestion collect in a *cloaca* before being expelled from the body.

Or consider one antelope's digestive system. Fall through winter, on the mountain ridges from central Canada into northern Mexico, you will see pronghorn antelope browsing on wild sage. In spring, they move down to open grasslands or deserts and browse on new growth. The flattened crown of antelope molars, or cheek teeth, acts as a grinding platform (Section 26.10). It is much larger, proportionally, than the crown on your molars (Figure 41.4*a*). Why such a difference? Most likely, you do not brush your mouth against dirt as you eat, but an antelope does. Abrasive soil particles enter its mouth along with tough plant parts, so the crown tends to wear down quickly. Natural selection has favored more antelope crown to wear down.

Antelopes are **ruminants**, or hoofed mammals that have multiple stomach chambers in which cellulose is slowly digested (Figure 41.4*b*). The chambers steadily accept food during extended periods of feeding, then slowly release nutrients when the animal rests.

Compared to ruminants, the meat-eating carnivores tend to have shorter intestines. Their enzymes cannot digest tough plant parts, but they make short work of meat. The stomach of many carnivores and scavengers expands to accept a lot of food in a single sitting. For instance, a male lion weighing 250 kilograms can eat as much as 40 kilograms of meat at one feeding. After gorging, it does not have to hunt again for some time. Between kills, stored nutrients are released, processed, and distributed in controlled ways.

Digestive systems mechanically and chemically break up food into small molecules that can be absorbed, along with ingested water, into the internal environment. They also expel undigested residues from the body.

Incomplete digestive systems are a saclike cavity with only one opening. Complete digestive systems are a tube with two openings and regional specializations in between.

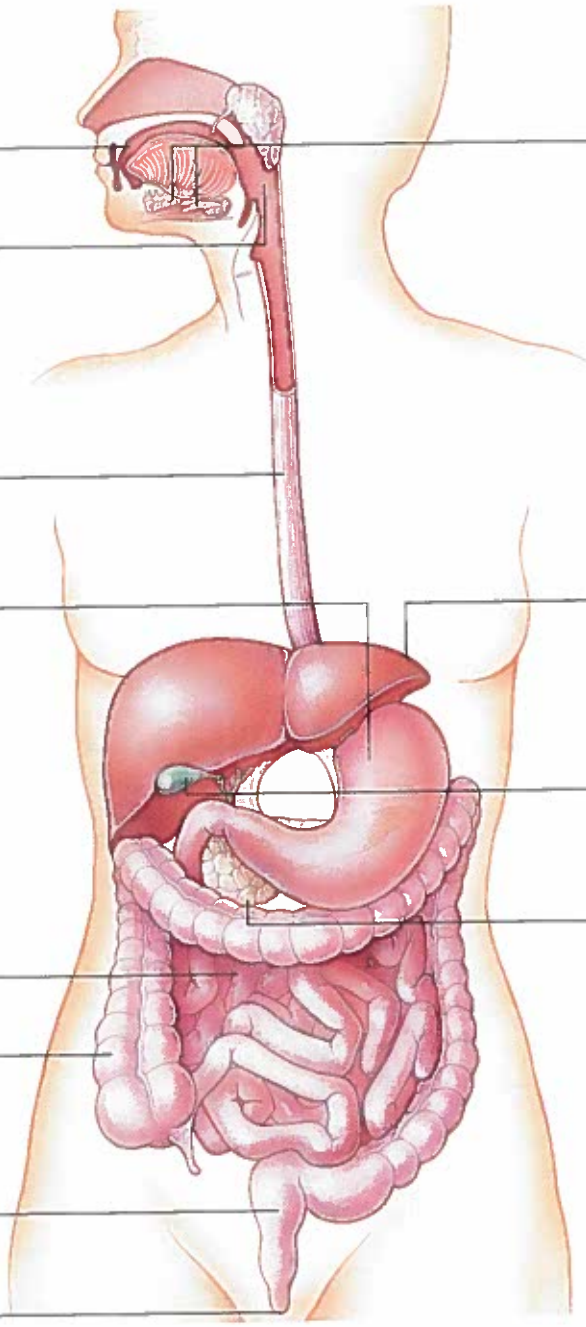
Digestive systems are adapted in ways that suit different species to their particular diet and style of feeding.

41.2 Overview of the Human Digestive System

NKS TO
CTIONS
39.2, 40.4

If it were fully stretched out in a straight line, the complete digestive system of an adult human would extend 6.5 to 9 meters (21 to 30 feet). That is one big tube! At different regions along its length, accessory glands and organs secrete enzymes and other substances that are required for digestion of food in the tube's lumen.

Figure 41.5 shows the complete digestive system of humans. All along the tube, mucus-coated epithelium is exposed to the lumen. Its thick, moist mucus helps protect the wall of the digestive tract and promotes diffusion of materials across its inner lining, into the internal environment.



a Major Components

MOUTH (ORAL CAVITY)
Entrance to system; food is moistened and chewed, polysaccharide digestion starts.

PHARYNX
Entrance to tubular part of system (and to respiratory system); moves food forward by contracting sequentially.

ESOPHAGUS
Muscular, saliva-moistened tube that moves food from pharynx to stomach.

STOMACH
Muscular sac; stretches to store food taken in faster than can be processed; gastric fluid mixes with food and kills many pathogens; protein digestion starts. Secretes ghrelin, an appetite stimulator.

SMALL INTESTINE
First part (duodenum, C-shaped, about 10 inches long) receives secretions from liver, gallbladder, and pancreas.
In second part (jejunum, about 3 feet long), most nutrients are digested and absorbed.
Third part (ileum, 6–7 feet long) absorbs some nutrients; delivers unabsorbed material to large intestine.

LARGE INTESTINE (COLON)
Concentrates and stores undigested matter by absorbing mineral ions, water; about 5 feet long. Divided into ascending, transverse, and descending portions.

RECTUM
Distension stimulates expulsion of feces.

ANUS
End of system; terminal opening through which feces are expelled.

b Accessory Organs

SALIVARY GLANDS
Glands (three main pairs, many minor ones) that secrete saliva, a fluid with polysaccharide-digesting enzymes, buffers, and mucus (which moistens food and lubricates it).

LIVER
Secretes bile (for emulsifying fat); roles in carbohydrate, fat, and protein metabolism.

GALLBLADDER
Stores and concentrates bile that the liver secretes.

PANCREAS
Secretes enzymes that break down all major food molecules; secretes buffers against HCl from the stomach. Secretes insulin, a hormonal control of glucose metabolism.

Figure 41.5 ***Animated!*** Overview of (**a**) major organs and (**b**) accessory organs of the human digestive system, together with a list of their primary functions.

Muscle contractions directionally propel substances from the mouth, on through the pharynx, esophagus, and gastrointestinal tract, or **gut**. In humans, the gut starts at the stomach and extends through the small intestine, the large intestine (or colon) and rectum, to the anus. Salivary glands and a liver, gallbladder, and pancreas are accessory organs. They secrete enzymes and other substances into specific gut regions.

Food is partially processed in the mouth, which has a tongue positioned above its floor. The membrane-covered skeletal muscles of this organ have roles in positioning food, swallowing, and speech. Its surface has an abundance of chemoreceptors that function in the sense of taste (Section 35.3). When you swallow, you force food into a **pharynx**, the tubular entrance to the esophagus *and* a trachea, the airway to the lungs. To keep food from going down the trachea, a flaplike valve—the epiglottis—and the vocal cords close it off to prevent choking. They stop you from breathing as food is being swallowed (Section 40.4 and page 717).

From the pharynx, contractions propel food down a muscular tube, the **esophagus**, and past a sphincter at the entrance to the **stomach**. A *sphincter* is a ring of smooth muscles at some point along a tube or at one of its openings. Muscle contractions narrow the tube diameter and thereby interrupt the forward or reverse movement of the tube's content.

The stomach empties into the **small intestine**. The action of smooth muscle layers inside the wall of both organs breaks apart, mixes, and propels food onward. Digestive enzymes and other secretions enter the gut lumen and go to work. Carbohydrate digestion starts in the mouth; protein digestion starts in the stomach. *But digestion of nearly all carbohydrates, lipids, proteins, and nucleic acids is completed in the small intestine, which also absorbs most of the released nutrients.*

In the **large intestine**, or colon, water and ions are absorbed, which compacts the undigested residues. In the last part of the human gut, the **rectum**, wastes are briefly stored before being expelled through an **anus**, the terminal opening.

Humans have a complete digestive system. Swallowing forces food and water in the mouth into the pharynx. Food continues through an esophagus to the stomach.

Carbohydrate digestion starts in the mouth and protein digestion starts in the stomach. Digestion is completed and nutrients are absorbed in the small intestine. The colon absorbs water and ions. The rectum stores compacted waste before its expulsion through the anus.

41.3 Prepping Food in the Mouth

In adult humans, thirty-two teeth and saliva interact in mechanically and chemically prepping food in the mouth.

LINKS T
SECTION
26.10, 26

A human **tooth** is a hardened jaw appendage (Figure 41.6). It has a coat of calcium deposits (enamel), dentin (a thick, bonelike layer), and a pulpy matrix serviced by a nerve and blood vessels. Chisel-shaped incisors shear chunks off food. Cone-shaped canines tear at it. The broad crowns and cusps of premolars and molars grind and crush it (Sections 26.10 and 26.12).

Pairs of salivary glands in back of the tongue and beneath it secrete saliva through ducts that open onto the surface of the oral cavity's lining. Saliva is mostly water in which salivary amylase, mucins, bicarbonate (HCO_3^-), and other substances are dissolved. Salivary amylase digests starch. HCO_3^- buffers acidic foods and helps maintain pH. Mucins are proteins in mucus that bind partially mashed food into a softened ball.

Teeth mechanically break food into particles and interact with the tongue to mix and soften it with saliva. Salivary enzymes partially break down carbohydrates in food.

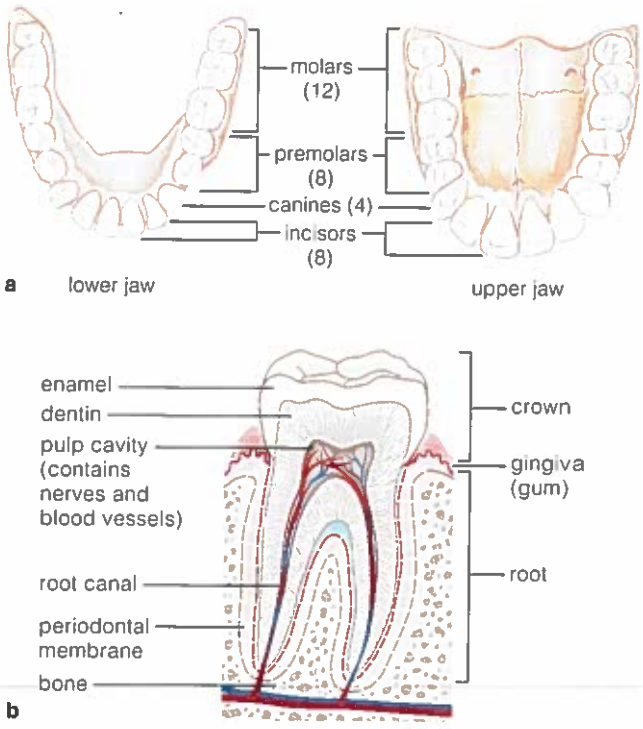


Figure 41.6 (**a**) Number and arrangement of human teeth. (**b**) A molar's main regions are a crown and root. The calcium-rich enamel on the crown is the hardest substance in the body. Section 39.2 explains what happens when bacteria infect the junction between a tooth and gum tissue.

41.4 Food Breakdown in the Stomach and Small Intestine

LINKS TO SECTIONS 3.3–3.6, 34.8

In the stomach and small intestine, digestive enzymes and other secretions help break down nutrients into fragments, then into molecules small enough to be absorbed.

Figures 41.7 and 41.8 show the smooth muscle layers inside the wall of the stomach and small intestine. The propulsive force of their contractions mixes digestive enzymes with the contents of the lumen (Table 41.1). Again, carbohydrate breakdown *starts* in the mouth. Protein breakdown *starts* in the stomach. But the small intestine completes the digestion of carbohydrates and proteins, and it also digests lipids and nucleic acids.

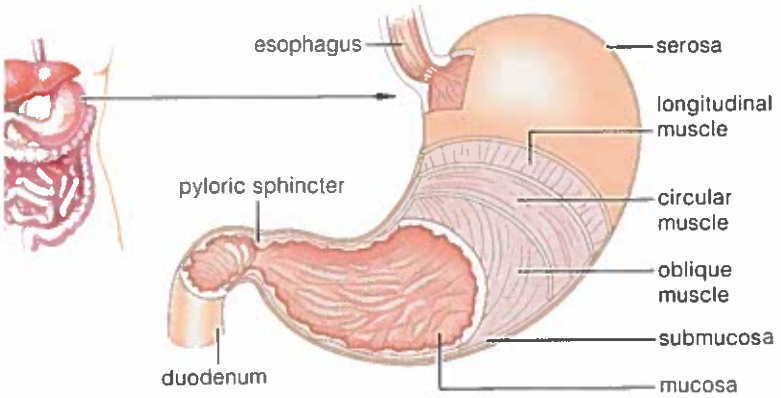


Figure 41.7 Structure of the stomach wall. Like most of the gut wall, it has an inner mucosa resting on a connective tissue with a mesh of nerves inside that locally controls digestion. Next to this tissue are smooth muscle layers that differ in orientation, hence in direction of contraction. The wall's outer layer of connective tissue is the serosa.

DIGESTION IN THE STOMACH

The stomach is a muscular, stretchable sac with three functions. It mechanically mixes ingested food, which it can store briefly. It secretes substances that dissolve and degrade food, especially proteins. It helps control the passage of food into the small intestine.

Glandular epithelium lines the inner stomach wall. Each day, its cells secrete about two liters of mucus, hydrochloric acid (HCl), pepsinogens, and some other components of **gastric fluid**. This fluid has a pH of 2 (Section 2.6). Strong contractions of the smooth muscle layers in the stomach wall mix this acidic fluid with food and form a partially digested, semiliquid mass called chyme. The high acidity kills some foodborne pathogens. It makes proteins unfold, which exposes peptide bonds (Section 3.5). It converts pepsinogens to pepsins—the enzymes that cleave peptide bonds. In this way, smaller polypeptides accumulate inside the stomach lumen. Also, some cells in the stomach wall release gastrin, a hormone that induces other cells to secrete HCl and pepsinogen. Peptic ulcers start when digestive enzymes and gastric fluid erode the lining of the stomach and small intestine (page 737).

The stomach empties by waves of contraction and relaxation. The waves mix chyme and gather force as they approach the pyloric sphincter, which is located between the stomach and small intestine (Figure 41.7). When a strong contraction closes the sphincter, most of the chyme gets forced back. Chyme enters the small intestine only in small, controllable amounts.

Table 41.1 Major Digestive Enzymes and Their Breakdown Products

Enzyme	Source	Where Active	Substrate	Main Breakdown Products
Carbohydrate Digestion				
Salivary amylase	Salivary glands	Mouth, stomach	Polysaccharides	Disaccharides
Pancreatic amylase	Pancreas	Small intestine	Polysaccharides	Disaccharides
Disaccharidases	Intestinal lining	Small intestine	Disaccharides	MONOSACCHARIDES* (such as glucose)
Protein Digestion				
Pepsins	Stomach lining	Stomach	Proteins	Protein fragments
Trypsin and chymotrypsin	Pancreas	Small intestine	Proteins	Protein fragments
Carboxypeptidase	Pancreas	Small intestine	Protein fragments	AMINO ACIDS*
Aminopeptidase	Intestinal lining	Small intestine	Protein fragments	AMINO ACIDS*
Fat Digestion				
Lipase	Pancreas	Small intestine	Triglycerides	FREE FATTY ACIDS, MONOGLYCERIDES*
Nucleic Acid Digestion				
Pancreatic nucleases	Pancreas	Small intestine	DNA, RNA	NUCLEOTIDES*
Intestinal nucleases	Intestinal lining	Small intestine	Nucleotides	NUCLEOTIDE BASES, MONOSACCHARIDES*

* Breakdown products small enough to be absorbed into the internal environment.

DIGESTION IN THE SMALL INTESTINE

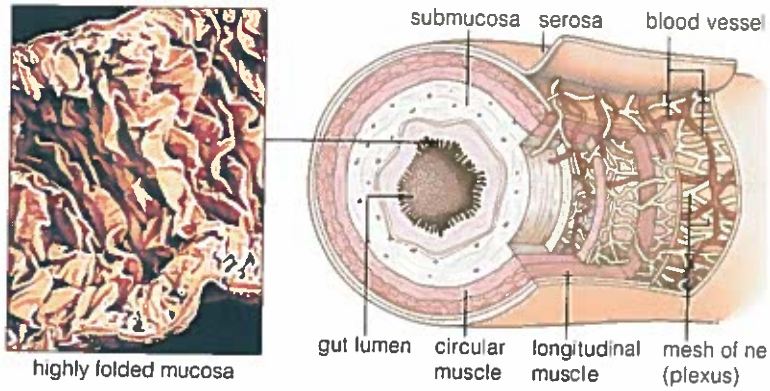
The small intestine has three regions: the duodenum, jejunum, and ileum (Figure 41.5). Each day, about nine liters of fluid enter the duodenum from the stomach and three glandular organs: the liver, gallbladder, and pancreas. At least 95 percent of the fluid is absorbed across the intestinal lining, the mucosa (Figure 41.8*a*).

Intestinal and pancreatic enzymes break down the large organic compounds in food to monosaccharides, monoglycerides, fatty acids, amino acids, nucleotides, and nucleotide bases. For instance, pancreatic enzymes called trypsin and chymotrypsin digest proteins into peptides, as pepsin does. Others break down peptides to free amino acids. In addition, the pancreas secretes bicarbonate, which helps to neutralize HCl. The small intestine is less acidic than the stomach because of it.

Lipases (pancreatic enzymes) and **bile** digest fats. Water, bile salts and pigments, cholesterol, and the phospholipid lecithin make up bile, which the liver secretes. After the stomach has emptied, a sphincter closes the main bile duct from the liver. Bile backs up into the gallbladder, which stores and concentrates it.

Bile salts enhance fat digestion by **emulsification** of fat droplets. Most fats in food are triglycerides. The triglycerides, which are insoluble in water, tend to cluster together as fat globules. But rings of circular muscles in the wall of the small intestine contract in an oscillating pattern known as **segmentation** (Figure 41.8*b*). While the contractions mix chyme, fat globules break up into small droplets that become coated with bile salts. Because bile salts bear negative charges, the coated droplets repel each other and stay separated. Tiny fat droplets suspended in fluid is the emulsion.

Compared to large fat globules, emulsion droplets offer fat-digesting enzyme molecules a greater surface area. Enzymes break down triglycerides faster to fatty acids and monoglycerides. In the next section, you will see how these products of digestion are absorbed.



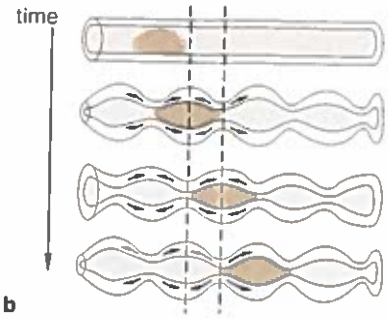


Figure 41.8 (**a**) Structure of the small intestine. Its wall has a highly folded inner lining, the mucosa. (**b**) Rings of circular muscle in the wall contract and relax in a pattern called segmentation. The pattern of back-and-forth movement propels, mixes, and forces chyme against the wall, which enhances both digestion and absorption.

CONTROLS OVER DIGESTION

The nervous system, endocrine system, and meshes of nerves in the gut wall control the pace of digestion. When food is distending the stomach wall, it activates mechanoreceptors, and signals flow along short reflex pathways to the smooth muscles and glands in local tissues. (Longer reflex pathways also carry signals to the brain.) Gut wall muscles contract and glandular cells secrete enzyme-rich fluid into the intestinal tract or hormones into blood. The responses depend partly on the chyme volume and composition. When a large meal activates many mechanoreceptors, contractions become more forceful and the stomach empties faster. High acidity or a high fat content in chyme triggers hormonal secretions that can slow stomach emptying.

Take stock of the gastrointestinal hormones. Again, gastrin stimulates HCl and pepsinogen secretion. The CCK you read about in the chapter introduction calls for the release of pancreatic enzymes and gallbladder contractions that squirt bile into the small intestine. Secretin induces the pancreas to release bicarbonate. Gastric inhibitory peptide (GIP) slows the contraction of intestinal muscles and increases cellular uptake of glucose by calling for insulin secretion.

During intense activity or stress, remember, signals from sympathetic neurons cause smooth muscle layers in the gut wall to contract more slowly (Section 34.8). The slowdown delays digestion as well as the passage of chyme to another part of the tube. If a person has a digestive disorder, chronic stress can aggravate it.

Gastric fluid, digestive enzymes, and wall contractions of the stomach and small intestine combine to break down nearly all food into bits small enough to be absorbed.

Signals from the nervous system, nerves in the gut wall, and hormones exert control over digestion.

41.5 Absorption From the Small Intestine

NKS TO
CTIONS
, 5.3–5.5,
38.1, 38.5

Folds and projections from cell surfaces of the small intestine enormously increase the surface area for interactions with chyme and for nutrient absorption.

FROM STRUCTURE TO FUNCTION

Think back on Section 25.2. When animals were first evolving, novel body shapes emerged in response to constraints imposed by the surface-to-volume ratio. Some epithelial cells became structurally dedicated to absorption. Threadlike absorptive structures formed at their free surface and became the first **microvilli** (singular, microvillus). The same constraint influenced the evolution of the intestinal mucosa—the structure of which clearly reflects its absorptive function.

Figure 41.9*a* shows the small intestine's profusely folded lining. Millions of **villi** (singular, villus) cover the surface. Each of these absorptive structures is one millimeter or so long. One lymph vessel starts near its tip. One arteriole leads into it; one venule leads out.

Different types of cells secrete mucus, hormones, bicarbonate, and the bacteria-killing lysozyme (Figure 41.9*b*). Others, the "brush border cells," have as many as 1,700 microvilli on their free surface. Without that immense intestinal surface area, nutrient absorption would be far too slow to sustain human life.

WHAT ARE THE ABSORPTION MECHANISMS?

Water and Solute Absorption Each day, a typical diet puts 1 to 2 liters of fluid in the small intestine, which also receives 6 to 7 liters of secretions from the stomach, accessory glands, and its own lining. About 80 percent of the water is absorbed, by way of osmosis, before it can even get to the colon. Said another way, absorption of water depends on solute concentration gradients across the lining (Section 5.5). Sodium ions (Na^+) play several roles in absorption.

Remember membrane transport proteins (Section 5.4)? Cotransporters passively shuttle Na^+ from the lumen into epithelial cells, along with simple sugars and amino acids. Then sodium–potassium pumps on

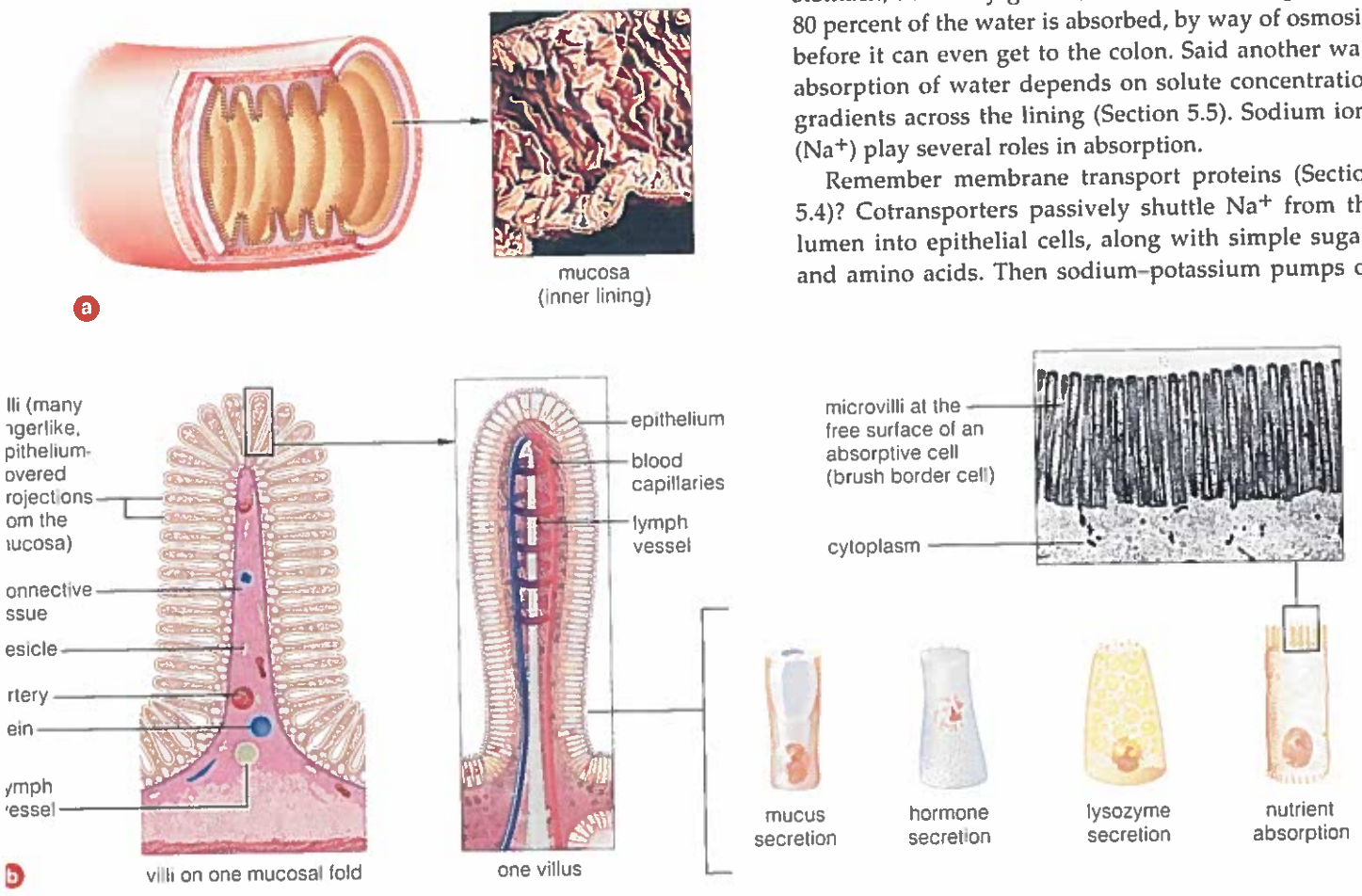


Figure 41.9 *Animated!* **(a)** Structure of the lining of the small intestine, the mucosa. The repetitive circular folds of this inner lining are permanent.

b) At the free surface of each mucosal fold are many absorptive structures called villi, fingerlike structures that contain blood capillaries and lymph vessels. Several types of epithelial cells with specialized functions cover the free surface of each villus. At the free surface of one type, the absorptive cells, a crown of microvilli extends into the intestinal lumen.

the opposite side of the cell actively transport Na^+ out, into interstitial fluid in the villus. Na^+ in the lumen also leaks past less-than-tight junctions between cells.

An Na^+ concentration gradient results, which sets up an osmotic gradient that attracts water out of the lumen, into or between the intestinal cells, then into the blood capillary inside the villus (Figure 41.10*b*).

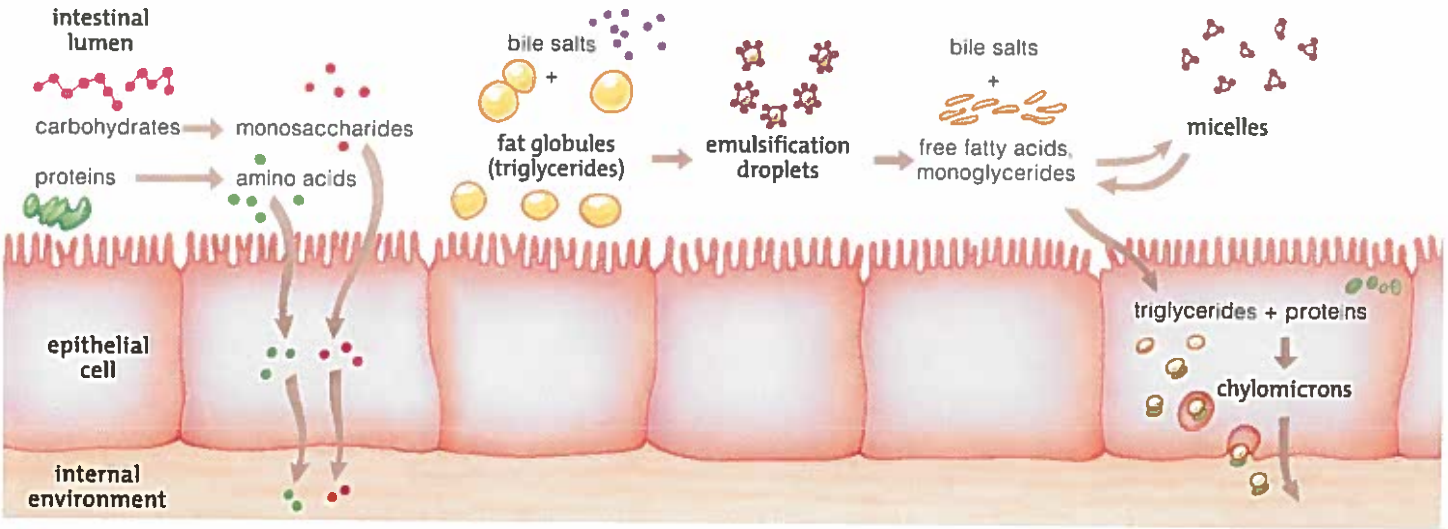
Brush border cells have several kinds of sodium-dependent transporters. For instance, SGLUT–1, one of the passive cotransporters, gets glucose and sodium into the cells, but never separately. When it binds Na^+, its shape changes in a way that opens a binding site for glucose. Glucose binding changes the transporter shape in a way that puts Na^+ and glucose in the cell. SGLUT–2 helps glucose, galactose, and fructose diffuse out of brush border cells and into interstitial fluid.

Fat Absorption Fatty acids and monoglycerides, the lipid-soluble products of fat digestion, diffuse across the lipid bilayer of brush border cells. Those bile salts introduced in Section 41.4 help (Figure 41.10*c–f*). By a process of **micelle formation**, bile salts combine with fatty acids in tiny droplets, or micelles. Molecules that make up micelles continuously exchange places with those suspended in chyme—but the point of micelles is to *concentrate* them in the fluid next to the mucosa. When they become concentrated enough, they diffuse down their gradients—from micelles into the brush border cells. In these cells, monoglycerides and fatty acids recombine as tryglycerides. Then triglycerides combine with proteins into particles—chylomicrons—which move to the plasma membrane inside exocytic vesicles. They are released into interstitial fluid.

Once absorbed, glucose and amino acids directly enter blood vessels. Triglycerides enter lymph vessels that eventually drain into the general circulation. The bloodstream then distributes the absorbed products of digestion throughout the body, along the circuits described in Sections 38.1 and 38.5.

With its richly folded mucosa, millions of villi, and many hundreds of millions of microvilli, the small intestine has a vast surface area for absorbing water and nutrients.

Substances diffuse through or in between brush border cells that line the free surface of each villus. Passive and active transport mechanisms help water and solutes cross; micelle formation helps lipid-soluble products cross.



a Enzymes secreted by the pancreas and cells of the epithelial lining complete the digestion of carbohydrates to monosaccharides, and proteins to amino acids.

b Sodium-dependent transporters move monosaccharides and amino acids across the plasma membrane of brush border cells of the intestinal lining, then out of the same cells and into the internal environment.

c Movement of the intestinal wall breaks up fat globules into small droplets. Bile salts prevent the globules from re-forming. Pancreatic enzymes digest the droplets to fatty acids and monoglycerides.

d Micelles form as bile salts combine with digestion products and phospholipids. Products can readily slip into and out of the micelles.

e Concentration of monoglycerides and fatty acids in micelles enhances gradients. This leads to diffusion of both substances across the lipid bilayer of the plasma membrane of cells making up the lining.

f Products of fat digestion reassemble into triglycerides in cells of the intestinal lining. These become coated with proteins, then are expelled (by exocytosis from the cells) into the internal environment.

Figure 41.10 *Animated!* Summary of digestion and absorption in the small intestine.

41.6 The Large Intestine

LINKS TO SECTIONS 4, 38.10, 39.2

Not everything that enters the small intestine can be or should be absorbed into the internal environment. The undigestible residues and other solid wastes become concentrated and stored before being eliminated.

Material not absorbed in the small intestine is moved into the large intestine, or **colon**. This part of the gut starts with a cup-shaped pouch (cecum). It ascends on the right side of the abdominal cavity, extends across to the other side, and descends and connects with the rectum (Figures 41.5 and 41.11). The colon concentrates and also stores feces: a mixture of water, bacteria, and undigested and unabsorbed material.

COLON FUNCTION

As waste material moves through the colon, it loses water and becomes more concentrated. As in the small intestine, cells of the intestinal mucosa transport Na^+ out of the lumen, and water follows by osmosis. The same cells secrete mucus, which lubricates feces and helps stop them from irritating the colon wall. They secrete bicarbonate, which buffers acidic products of enteric (gut-dwelling) bacteria. Generally, the bacteria are harmless unless they breach the wall of the colon and enter the abdominal cavity.

Bands of smooth muscle in the colon wall contract and relax. They move the lumen's contents back and forth against the wall's absorptive surface. Networks of nerves (plexuses) in the wall control the pattern of oscillation, which is similar to segmentation in the small intestine but much slower. The environment in the small intestine restricts bacterial growth, but the colon supports big populations of approximately 500 bacterial species. Some of the beneficial bacteria, such as *Escherichia coli*, make essential vitamins.

Bulk is the name for the volume of cellulose and all other undigested residues that cannot be decreased by absorption in the colon. It adds to the volume of material and slows transit time through the colon.

After a meal, gastrin and autonomic nerves make much of the ascending and transverse colon contract together. Within seconds, bulk is propelled through much of the colon's extensive length. It accumulates in the rectum. When it distends the rectal wall enough, it stimulates reflex expulsion. The nervous system can override the reflex by calling for the contraction of a sphincter at the anus, the last opening of the gut.

COLON MALFUNCTION

Expulsion from the rectum (defecation) occurs three times a day to once a week, on the average. Emotional stress, aging, a low-bulk diet, injury, or disease can delay it, a condition called *constipation*. The longer the slowdown, the more water leaves feces, which harden and dry. The result is abdominal discomfort, along with loss of appetite, headaches, and often nausea.

Hard feces may become lodged in the **appendix**, a narrow projection from the cecum (Figure 41.11). The appendix has no known digestive function. However, like the ileum, bacteria-fighting white blood cells are packed inside it. Bits of wastes can clog its opening. The outcome is *appendicitis*—an inflamed appendix. If that occurs, the appendix must be surgically removed. Otherwise it might rupture and let bacteria enter the abdominal cavity, where infections are dangerous.

Some people are genetically predisposed to develop *colon polyps*, or small projections from the colon wall. The polyps are benign growths, but some may later become cancerous. Colon cancer is highly curable but only if it is detected in time. Every year in the United States, about 50,000 people die from this cancer. Blood in feces and changes in bowel habits may be signs of colon cancer and should be reported to a doctor.

Colonoscopy is a diagnostic procedure. Clinicians use a camera at the end of a flexible tube to examine the colon for polyps or cancer. *Virtual colonoscopy* uses x-rays and a computer to generate images of the colon.

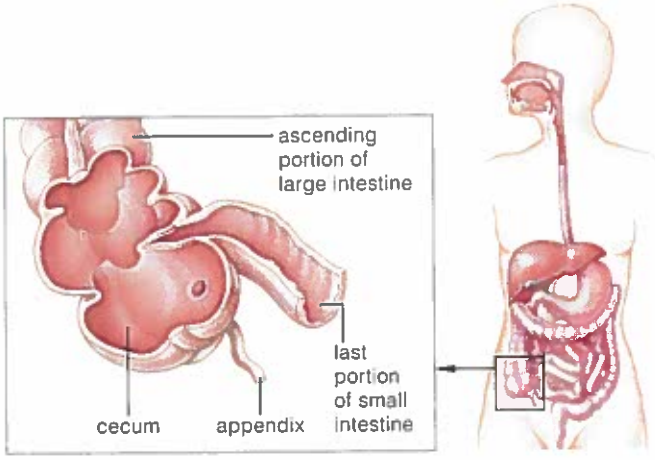


Figure 41.11 Cecum and appendix of the large intestine (colon).

The colon absorbs water and mineral ions. It also compacts undigested residues from food, enteric bacteria, and water into feces, which are stored in the rectum, the final part of the digestive tract.

41.7 What Happens to Absorbed Organic Compounds?

Small organic compounds—sugars, amino acids, and triglycerides—are absorbed from the small intestine. They are distributed to body cells and burned as fuel, stored, or used in synthesis of larger organic compounds.

In Sections 8.6 and 36.6, you considered mechanisms that help control *organic metabolism*, the disposition of glucose and other organic compounds in the body as a whole. You thought about some pathways by which carbohydrates, fats, and proteins are broken down to forms used as intermediates in aerobic respiration, an ATP producing pathway. Figure 41.12 rounds out the picture by showing all of the major routes by which organic compounds obtained from food are shuffled and reshuffled in the body as a whole.

All cells continually recycle some carbohydrates, lipids, and proteins by breaking them apart. They use breakdown products as energy sources and building blocks. This massive molecular turnover is integrated by the nervous and endocrine systems.

Reflect for a moment on a few crucial points about organic metabolism. When you eat, your body adds to its pool of raw materials. Excess carbohydrates and other organic compounds absorbed from the gut are transformed mostly into fats, which become stored in adipose tissue. Some are converted to glycogen in the liver and in all muscles. While the raw materials are being absorbed and stored, most cells use glucose as the main energy source. There is no net breakdown of protein in muscle tissue or any other tissue during this period, nor is there any net fat breakdown.

In between meals, the brain takes up two-thirds of the circulating glucose, so most body cells tap fat and glycogen stores. Adipose cells degrade fats to glycerol and fatty acids, which enter blood. Liver cells break down glycogen and release glucose, which also enters blood. Most body cells take up the fatty acids as well as the glucose for ATP production.

Remember the introduction to Chapter 6? The liver stores, converts, and maintains the concentrations of required organic compounds in blood. It inactivates most hormones, which it sends on to the kidneys for excretion in the urine. It also removes worn-out blood cells and deactivates certain toxins, including alcohol. Again, ammonia (NH_3) is a potentially toxic product of amino acid breakdown, but the liver converts it to a less toxic form, urea, that can be excreted in urine.

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Absorbed sugars are the human body's most accessible energy source. Between meals, the brain draws on glucose in blood; other cells tap fat and glycogen stores. Adipose cells convert and store excess carbohydrates as fats.

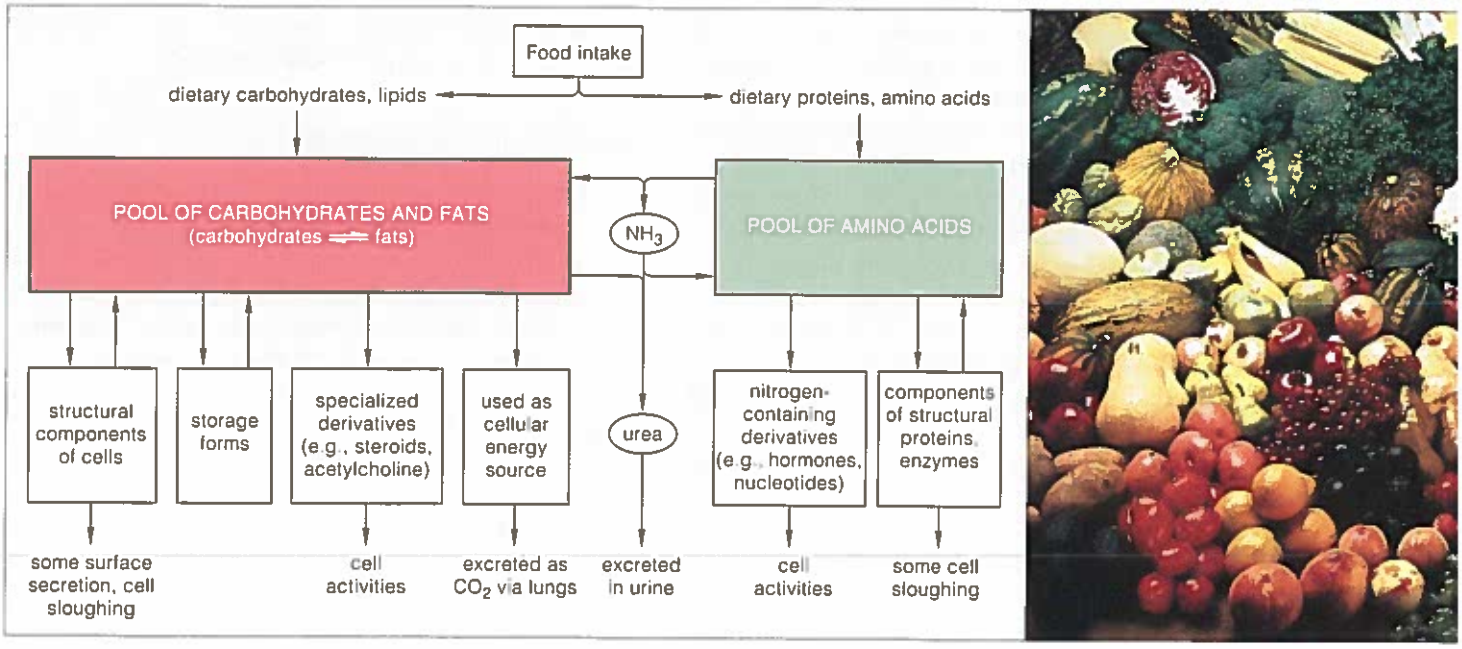

Figure 41.12 Summary of the major pathways of organic metabolism. Cells continually synthesize and tear down carbohydrates, fats, and proteins. Most urea forms in the liver.

41.8 Human Nutritional Requirements

LINKS TO SECTIONS 3, 36.6, 38.9

There is an old saying, "You are what you eat," which is meant to imply that diet profoundly affects your body's structure and function. So what do you eat?

USDA DIETARY RECOMMENDATIONS

The United States Food and Drug Administration has now issued a set of nutritional guidelines to replace its earlier "food pyramid." These guidelines are based on extensive research into nutrition. They are designed to educate people on how good dietary choices can reduce the risk for chronic diseases, such as diabetes, hypertension, heart disease, and certain cancers. The recommended number of servings for different food groups are shown in Figure 41.13.

In stark contrast to the diet of a typical American, the new guidelines recommend lowering the intake of refined grains, saturated fats, *trans*-fatty acids, added sugar or caloric sweeteners, and salt (no more than a teaspoon per day). They also recommend eating more vegetables and fruits with a high potassium and fiber content, fat-free or low-fat milk products, and whole grains. If you wish, you can download the complete FDA report from www.health.gov.

The new USDA guidelines call for about 55 percent of daily caloric intake to come from carbohydrates.

A CARBOHYDRATE–INSULIN CONNECTION

Complex carbohydrates are readily broken down to glucose, the body's main source of energy. Starch is abundant in fleshy fruits, cereal grains, and legumes, such as peas and beans. Foods that are rich in complex carbohydrates are typically also high in fiber, which helps to prevent constipation and colon problems. As epidemiologist Denis Burkitt has put it, when people pass small volumes of feces, you have large hospitals.

Unlike complex carbohydrates, simple sugars do not provide any fiber, vitamins, or minerals. Also, highly refined carbohydrates have a *high glycemic index*. This means that within minutes of being absorbed, refined carbohydrates cause an upsurge in the blood levels of sugar and insulin.

An insulin surge makes cells take up sugar quickly (Section 36.6). A few hours later, the level of sugar in blood is lower than before, and so we feel hungry. But the circulating insulin keeps cells from dipping into stores of fat. Cells metabolize fat only when insulin is low. So we eat more, secrete more insulin, and keep on storing fat—mainly in the form of triglycerides. Over time, high triglyceride levels increase the risk of heart disease and type 2 diabetes.

High intake of soft drinks and other products with a lot of fructose corn syrup is a concern. A product that is sweetened with glucose stimulates adipose cells to secrete leptin and the stomach to secrete less ghrelin, so the sense of hunger diminishes. By contrast, high-fructose products have no effect on leptin and ghrelin secretion. Even though fructose has the same amount of calories as glucose, a person still feels hungry.

GOOD FAT, BAD FAT

You cannot stay alive without fats. Cell membranes incorporate the phospholipid lecithin. Also, other fats act as energy reserves, cushion many internal organs, and provide insulation beneath the skin. Dietary fats help store fat-soluble vitamins. However, the body can make most of its own fats by converting proteins and carbohydrates. The ones that it cannot make, such as linoleic acid, are **essential fatty acids**. A teaspoonful or two each day of some polyunsaturated fat, such as olive oil and corn oil, may turn out to be enough of a dietary fat supplement.

Like other animal fats, butter is a saturated fat and contains cholesterol. This sterol is a precursor for the synthesis of bile acids and steroid hormones. Animal cell membranes require it. However, too much dietary cholesterol gets transported in blood in a form (LDL) that may invite heart disease and stroke. Section 38.9 has more on "good" and "bad" forms of cholesterol. For now, it is enough to keep this new FDA guideline in mind: Total fat intake should not exceed 20 to 30 percent of the total daily caloric intake.

BODY-BUILDING PROTEINS

Your body also cannot function without proteins. It requires amino acid components of dietary proteins for its own protein-building programs. Of the twenty common types, eight are **essential amino acids**. Your cells cannot synthesize them. Such amino acids must make up a small portion of the total protein intake. Those eight are methionine (or cysteine, its metabolic equivalent), isoleucine, leucine, lysine, phenylalanine (tyrosine), threonine, tryptophan, and valine.

Most proteins in animal tissues are *complete*; their amino acid ratios match a human's nutritional needs. Nearly all plant proteins are *incomplete*, in that they lack one or more amino acids that are essential for humans. The proteins of quinoa (*Chenopodium quinoa*) are one of the notable exceptions (Section 32.9). In parts of the world where animal protein is a luxury, traditional cuisines include fine combinations of plant

USDA Nutritional Guidelines

Food Group	Amount Recommended
Vegetables	2 5 cups/day
Dark green vegetables	3 cups/week
Orange vegetables	2 cups/week
Legumes	3 cups/week
Starchy vegetables	3 cups/week
Other vegetables	6.5 cups/week
Fruits	2 cups/day
Milk Products	3 cups/day
Grains	6 ounces/day
Whole grains	3 ounces/day
Other grains	3 ounces/day
Fish, poultry, lean meat	5.5 ounces/day
Oils	24 grams/day

Figure 41.13 From the United States Department of Agriculture, a summary of nutritional guidelines, as of 2006. The recommended proportions add up to a daily 2,000 kilocalorie intake for sedentary females between ages ten and thirty. Recommended intake and serving sizes are larger for males and highly active females and less for older females. The USDA recommends varying protein choices (fish, poultry, lean meats, eggs, beans, nuts, and seeds).

proteins, particularly beans with rice, cornbread with chili, tofu with rice, and lentils with wheat bread.

REGARDING THE ALTERNATIVE DIETS

Even with new FDA guidelines in place, alternative diets still abound. The *Mediterranean diet* pyramid, for instance, has a big base of grain products, then fruits and vegetables, legumes and nuts, then *olive oil* as the fat group, then cheese and yogurt. The pyramid limits weekly intakes of fish, poultry, eggs, simple sugars, and—at its tiny top—red meat. Olive oil represents 40 percent of the diet's total energy intake. Because it is monounsaturated, olive oil is less likely to raise the blood cholesterol level, compared to saturated fats. It also is an antioxidant that helps remove free radicals. You might call this an "olive oil is good" diet.

Low-carb diets, too, are still wildly popular. About 10 million Americans report that they are following a program that calls for reduced carbohydrate intake and a greater intake of proteins and fats. Such diets actually can promote rapid weight loss. However, the long-term effects are being debated—often heatedly—by health professionals.

Again, ammonia that forms as proteins are digested can be toxic. Liver enzymes convert it to urea, which kidneys filter from blood and excrete, in urine. When the body taps into fats instead of carbohydrates as the main energy source, metabolic wastes called ketones enter blood. These ketones are acidic and must be filtered out of blood and excreted. The kidney has to work harder to filter them. Two of the possible outcomes are kidney stones and damage to the kidney's blood-filtering units (nephrons). Anyone who has impaired kidney function should avoid a high-protein diet.

Some nutritionists are concerned that low-carb diets promote increased consumption of saturated fats, which can raise the blood cholesterol levels. However, as many studies indicate, adhering to a low-carb diet for six months does not raise the level of LDLs ("bad" cholesterol). In some cases, blood cholesterol levels actually decreased. Still, given the amount of evidence that a diet high in saturated fat increases the risks of heart disease, low-carb dieters are advised to select lean cuts of meats and fish over fattier, high-protein foods.

In short, even with new government guidelines, we still do not have all the nutritional answers.

For three decades, nutritionists have been advocating a low-fat, high-carbohydrate diet. Too many individuals have mistakenly taken "carbohydrate" to mean it is acceptable to load up on refined sugars and starches.

New government guidelines reflect major shifts in nutritional recommendations.

41.9 Vitamins and Minerals

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.4, 23.11

Think back on the outcomes of vitamin A deficiency, as sketched out in the Chapter 16 introduction. This is not an isolated problem. Chronically inadequate or excess amounts of most vitamins and minerals can disrupt normal development and metabolism.

Vitamins are *organic* substances that are essential for growth and survival; no other substance can carry out their metabolic functions. Unlike most plant species, which synthesize all the vitamins they require, most animals lost the ability to do so and must obtain all vitamins from their food. At a minimum, human cells require the thirteen vitamins listed in Table 41.2. Each type has specific metabolic roles. For instance, it takes niacin, a B vitamin, to make the vital coenzyme NAD.

Minerals are *inorganic* substances that are essential for growth and survival because no other substances can serve their metabolic functions. For instance, all of

Table 41.2 Major Vitamins: Sources, Functions, and Effects of Deficiencies or Excesses*

Vitamin	Common Sources	Main Functions	Effects of Chronic Deficiency	Effects of Extreme Excess
Fat-Soluble Vitamins				
A	Its precursor comes from beta-carotene in yellow fruits, yellow or green leafy vegetables; also in fortified milk, egg yolk, fish, liver	Used in synthesis of visual pigments, bone, teeth; maintains epithelia	Dry, scaly skin; lowered resistance to infections; night blindness; permanent blindness	Malformed fetuses; hair loss; changes in skin; liver and bone damage; bone pain
D	Inactive form made in skin, activated in liver, kidneys; in fatty fish, egg yolk, fortified milk products	Promotes bone growth and mineralization; enhances calcium absorption	Bone deformities (rickets) in children; bone softening in adults	Retarded growth; kidney damage; calcium deposits in soft tissues
E	Whole grains, dark green vegetables, vegetable oils	Counters effects of free radicals; helps maintain cell membranes; blocks breakdown of vitamins A and C in gut	Lysis of red blood cells; nerve damage	Muscle weakness, fatigue, headaches, nausea
K	Enterobacteria form most of it; also in green leafy vegetables, cabbage	Blood clotting; ATP formation via electron transport	Abnormal blood clotting; severe bleeding (hemorrhaging)	Anemia; liver damage and jaundice
Water-Soluble Vitamins				
B_1 (thiamin)	Whole grains, green leafy vegetables, legumes, lean meats, eggs	Connective tissue formation; folate utilization; coenzyme action	Water retention in tissues; tingling sensations; heart changes; poor coordination	None reported from food; possible shock reaction from repeated injections
B_2 (riboflavin)	Whole grains, poultry, fish, egg white, milk	Coenzyme action	Skin lesions	None reported
B_3 (niacin)	Green leafy vegetables, potatoes, peanuts, poultry, fish, pork, beef	Coenzyme action	Contributes to pellagra (damage to skin, gut, nervous system, etc.)	Skin flushing; possible liver damage
B_6	Spinach, tomatoes, potatoes, meats	Coenzyme in amino acid metabolism	Skin, muscle, and nerve damage; anemia	Impaired coordination; numbness in feet
Pantothenic acid	In many foods (meats, yeast, egg yolk especially)	Coenzyme in glucose metabolism, fatty acid and steroid synthesis	Fatigue, tingling in hands, headaches, nausea	None reported; may cause diarrhea occasionally
Folate (folic acid)	Dark green vegetables, whole grains, yeast, lean meats; enterobacteria produce some folate	Coenzyme in nucleic acid and amino acid metabolism	A type of anemia; inflamed tongue; diarrhea; impaired growth; mental disorders	Masks vitamin B_{12} deficiency
B_{12}	Poultry, fish, red meat, dairy foods (not butter)	Coenzyme in nucleic acid metabolism	A type of anemia; impaired nerve function	None reported
Biotin	Legumes, egg yolk; colon bacteria produce some	Coenzyme in fat, glycogen formation and in amino acid metabolism	Scaly skin (dermatitis); sore tongue; depression; anemia	None reported
C (ascorbic acid)	Fruits and vegetables, especially citrus, berries, cantaloupe, cabbage, broccoli, green pepper	Collagen synthesis; possibly inhibits effects of free radicals; structural role in bone, cartilage, and teeth; used in carbohydrate metabolism	Scurvy; poor wound healing; impaired immunity	Diarrhea, other digestive upsets; may alter results of some diagnostic tests

* Guidelines for appropriate daily intakes are being worked out by the Food and Drug Administration.