

CHAPTER 1

Mammalian nutrition

By the end of this chapter you should be able to:

- 1 explain what is meant by *heterotrophic nutrition*, and outline the basic principles;
- 2 explain what is meant by the terms *ingestion*, *digestion*, *absorption* and *egestion*;
- 3 distinguish between mechanical and chemical digestion;
- 4 state the sites of production and action, and explain the functions of: pepsin, trypsin, chymotrypsin, exopeptidases, amylases, maltase, lipase and bile salts;
- 5 recognise on photographs and diagrams, and by using the light microscope, the following main regions of the gut: stomach, ileum and colon;
- 6 describe the structure of the stomach and its functions in digestion and absorption;
- 7 describe the gross structure and histology of the pancreas and explain its functions as an exocrine gland;
- 8 describe the structure of the ileum and its functions in digestion and absorption;
- 9 describe the functions of the colon in absorption;
- 10 outline the roles of the nervous system and hormones in the control of digestion;
- 11 describe the specialisation of teeth and digestive systems in a cow (a ruminant) and a dog (a carnivore).

In *Biology 1*, we looked in detail at the human diet – what we need to eat and why. Humans, like all other animals (not only mammals) and all fungi, are **heterotrophs**. This means that we need to eat food containing organic molecules. These organic molecules, which include carbohydrates, fats and proteins, are our only source of energy. In contrast, **autotrophs** such as green plants do not need to take in any organic molecules at all. They obtain their energy from sunlight, and can use this energy to build organic molecules from inorganic ones. They produce carbohydrates from carbon dioxide and water, by photosynthesis (described in detail in chapter 2 in *Biology 2*) and can then use these carbohydrates, plus inorganic ions such as nitrate, phosphate and magnesium, to manufacture all the organic molecules that they require. Heterotrophs therefore depend on autotrophs for the supply of

organic molecules on which they feed. Some of them feed directly on plants, while others feed further along a food chain. But eventually all of our food can be traced back to green plants, and the energy of sunlight.

In this chapter, we will consider what happens to the food we eat as it travels through the alimentary canal, and also look at the diets and digestive systems of some mammals other than humans.

An overview of digestion

In humans, as in all mammals, digestion takes place within the **alimentary canal**. This is a long tube which runs from the mouth to the anus. In an adult, it is up to 6 m long, with some parts of it coiled round and round inside the abdomen. The

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alimentary canal, plus other organs that secrete various substances into it – the salivary glands, liver and pancreas – make up the **digestive system** (figure 1.1).

The space in the middle of the alimentary canal, like the space in the middle of any tube in the body, is known as a **lumen**. The lumen of the alimentary canal runs without obstruction from one end of the body to the other. Substances can pass right through without ever entering a cell. Technically, therefore, it can be considered to be part of the outside world. In order to enter the tissues of the body, food substances must move into the cells in the wall of the canal, from where most of them pass into the blood stream. This process is called **absorption**.

In general, only small molecules and ions can be absorbed through the walls of the alimentary canal. These include water, inorganic ions such as

iron and calcium, vitamins, amino acids and monosaccharides. Macromolecules such as starch and proteins cannot usually be absorbed, and they must first be broken down into small molecules – the monomers from which they are made – before absorption can take place. They are broken down by **hydrolysis** reactions, in a process called **chemical digestion**. A variety of different enzymes catalyse these reactions.

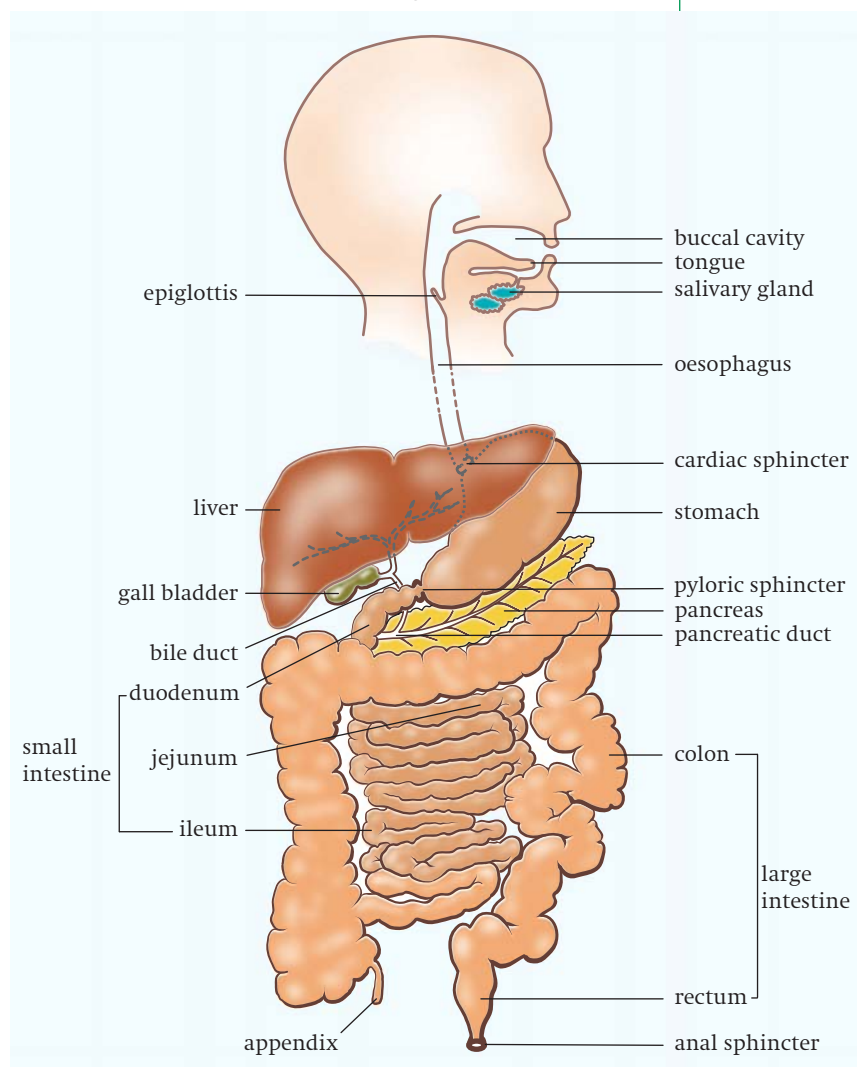
The enzymes get better access to the food materials within the alimentary canal if these materials are in small pieces, rather than large lumps. Humans – unlike some animals, such as dogs – normally chew their food before swallowing it, which helps to break up lumps of food into many smaller pieces with a larger surface area. Churning movements in the stomach also help with this. These two processes are sometimes known as **mechanical digestion**. So, mechanical digestion

breaks up large pieces of food into small ones, and is followed by chemical digestion which breaks up large *molecules* of food into small ones.

The entry of food into the alimentary canal is known as **ingestion**. This is followed by digestion, and then absorption. Any food that cannot be digested, such as the cellulose in plant cell walls, cannot be absorbed either, so it passes right through the alimentary canal and out through the anus, in the form of **faeces**. The removal of faeces from the body is called **egestion**. It is important not to confuse this with *excretion*, which is the removal of waste products of metabolism (substances that are made inside cells, such as urea and carbon dioxide) from the body. The great majority of the material in faeces has never been inside a cell, so cannot ever have been part of metabolism.

Enzymes and digestion

A number of different enzymes are secreted into the alimentary canal.



● **Figure 1.1** The human digestive system.

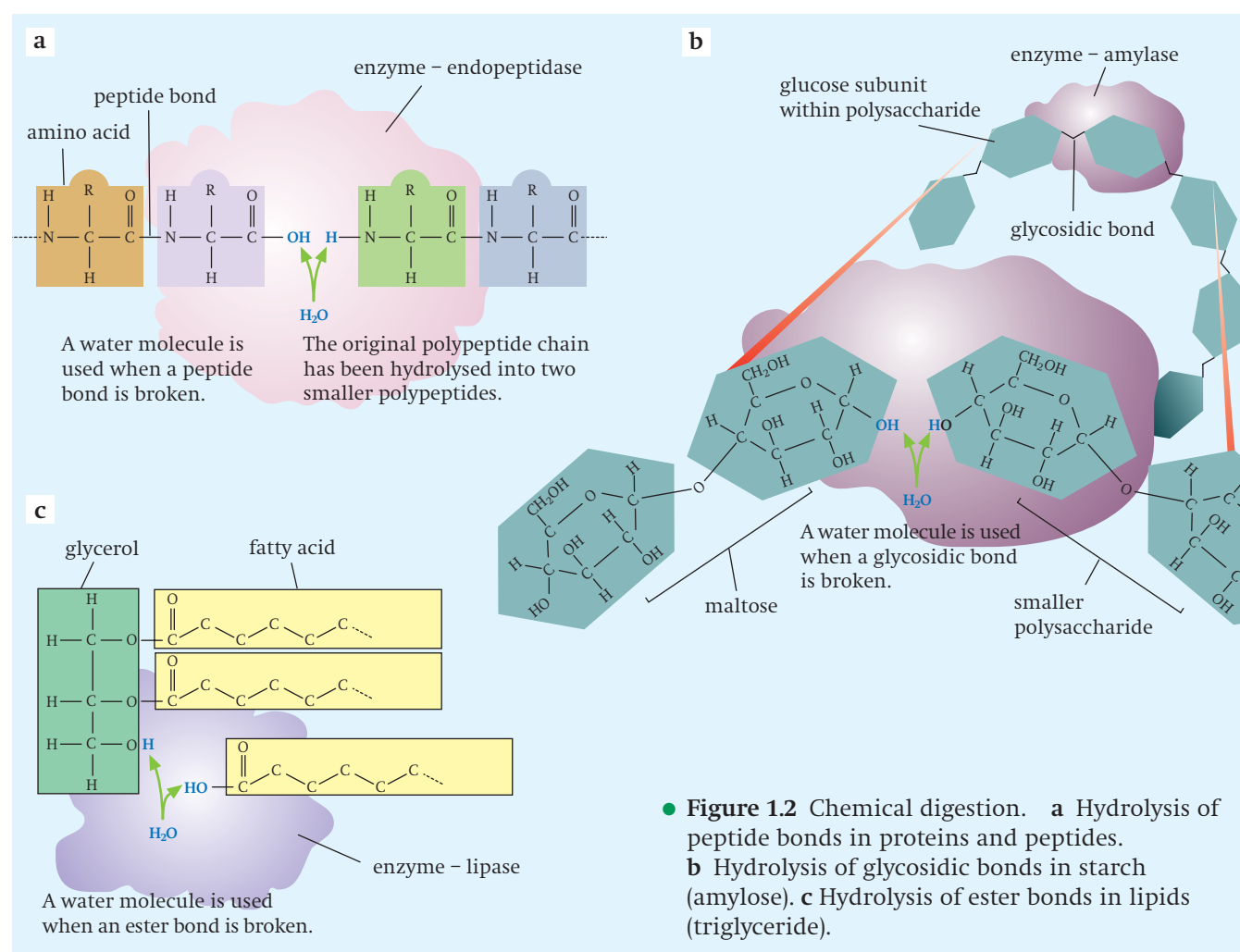
Before we look in detail at the events that take place within each of the sections of the alimentary canal, it may be helpful to take an overview of what these enzymes are, what they do and where they do it.

All of the reactions that take place during digestion are **hydrolysis** reactions – that is, they involve the breaking down of large molecules to small ones with the addition of water. *Figure 1.2* shows the hydrolysis reactions that occur when starch, proteins and fats are digested. All digestive enzymes are therefore **hydrolases**. They can be further classified according to the type of molecule that they break down. **Proteases** or **peptidases** catalyse the hydrolysis of proteins, **carbohydrases** the hydrolysis of carbohydrates and **lipases** the hydrolysis of lipids (*table 1.1*).

Protein digestion takes place in the stomach, duodenum and ileum. In the stomach, protein molecules are broken down into smaller lengths by the protease **pepsin**. Pepsin catalyses the hydrolysis

of some peptide bonds *within* protein molecules, so it is known as an **endopeptidase**. The result of this is therefore the breakdown of very long chains of amino acids into smaller lengths. When these arrive in the duodenum, they are acted on by two more proteases, **trypsin** and **chymotrypsin**. These two enzymes, like pepsin, are endopeptidases, breaking down the amino acid chains into even smaller lengths. These short chains are then acted on by yet another protease called **carboxypeptidase**. This behaves differently from the first three, catalysing the hydrolysis of the peptide bonds linking the end amino acids in the chain. Proteases that do this are called **exopeptidases**, and they produce single amino acids, which can then be absorbed into the blood capillaries in the walls of the small intestine.

Carbohydrate digestion begins in the mouth, where the enzyme **amylase** begins the breakdown of starch molecules into the disaccharide maltose. Nothing further happens to carbohydrates until



● **Figure 1.2** Chemical digestion. **a** Hydrolysis of peptide bonds in proteins and peptides. **b** Hydrolysis of glycosidic bonds in starch (amylose). **c** Hydrolysis of ester bonds in lipids (triglyceride).

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Region	Secretion	Enzyme	Substrate	Product
mouth	saliva from salivary glands	amylase	starch (amylose)	maltose
oesophagus	–	–	–	–
stomach	gastric juice from gastric glands	pepsin (endopeptidase)	protein	peptides
		lipase	lipids	fatty acids and glycerol
duodenum	pancreatic juice from pancreas	amylase	starch (amylose)	maltose
		trypsin (endopeptidase)	protein	peptides
		chymotrypsin (endopeptidase)	protein	peptides
		carboxypeptidase (exopeptidase)	peptides	amino acids
	lipase	lipids	fatty acids and glycerol	
	bile from liver	–	–	–
ileum	none – enzymes are produced by, and remain on the surface of, cells covering the villi	maltase	maltose	glucose
		sucrase	sucrose	glucose and fructose
		lactase	lactose	glucose and galactose
		peptidase (exopeptidase)	peptides	amino acids
Key: proteases carbohydrases lipases				

● Table 1.1 A summary of enzyme activity in the human alimentary canal.

the food reaches the duodenum, where more amylase is added to the food, completing the hydrolysis of starch to maltose. In the ileum, several enzymes are present that break down disaccharides to monosaccharides. In particular, **maltase** catalyses the hydrolysis of maltose to glucose; **sucrase** breaks down sucrose to glucose and fructose; and **lactase** breaks down lactose to glucose and galactose. These monosaccharides are then absorbed.

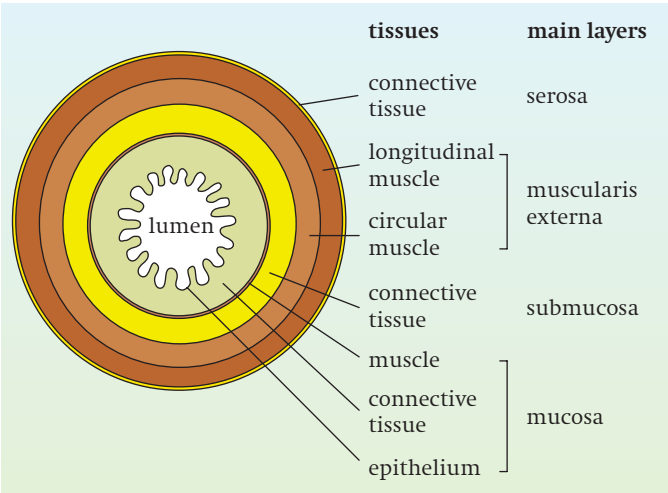
Lipid digestion begins in the stomach, where the enzyme **lipase** breaks triglycerides into fatty acids and glycerol. However, this process does not get very far in the stomach, and the majority of fat digestion takes place in the duodenum and ileum, where **pancreatic juice** containing more lipases flows in from the pancreas. Here, too, the greenish liquid called **bile** enters the alimentary canal. Bile contains no enzymes, but it does contain **bile salts** that help to disperse large drops of fat into such tiny droplets that they can mix with the watery liquids present in the lumen of the canal – a process known as **emulsification**. As

the lipases are water-soluble, this greatly increases the surface area of the lipids with which lipases can make contact. The breakdown of lipid molecules to fatty acids and glycerol is completed in the duodenum and ileum, where the products are absorbed.

The structure and function of the alimentary canal

The basic structure of the alimentary canal is the same throughout its length, apart from within the mouth. Its walls are made up of several different tissues arranged into four main layers, known as the mucosa, submucosa, muscularis externa and serosa (*figure 1.3*).

The **mucosa** is the layer nearest to the lumen. On its inner surface is a thin **epithelium**. In every part of the alimentary canal, this epithelium contains **goblet cells**, which secrete mucus to lubricate and protect the cells from abrasion by food, and from hydrolysis by



● **Figure 1.3** Diagrammatic transverse section through the alimentary canal to show the tissues that make up its walls.

digestive enzymes. However, in other respects the epithelium differs considerably in different regions of the alimentary canal, as we shall see. Beneath the epithelium, still part of the mucosa, is a layer of connective tissue, and beneath that a thin layer of smooth muscle, the **muscularis mucosa**. Smooth muscle, unlike the striated or voluntary muscle that is attached to the skeleton, is not under voluntary control. It is able to contract slowly and rhythmically for long periods without tiring.

The **submucosa** is made up of connective tissue, within which lie blood vessels and nerves. The connective tissue contains a high proportion of collagen and elastin (both fibrous proteins).

The **muscularis externa**, like the muscularis mucosa, is made up of smooth muscle. Here, however, the muscle is arranged in two bands, in one of which the fibres lie lengthwise along the wall of the canal – known as **longitudinal muscle** – and in one of which they lie around the wall –

known as **circular muscle**. The contraction and relaxation of these muscles moves the food through the alimentary canal by **peristalsis** (figure 1.4) and also helps to mix the food within the canal with the various secretions, by means of churning movements.

The **serosa** is a thin layer of connective tissue that makes up the outer layer of the wall.

The mouth and oesophagus

Food is ingested into the mouth using the teeth and lips. Chewing or **mastication**, using the broad ridges and grooves on the molars and premolars, breaks solid food into smaller pieces, thus increasing its surface area.

Saliva is secreted into the mouth from three pairs of **salivary glands**. Saliva is mostly water, and this helps to dissolve any soluble components in the food, allowing them to interact with receptors in the taste buds on the tongue, so that they can be tasted. Saliva also contains mucus, which helps the tongue to form the food into a small slippery ball or bolus for swallowing, and the enzyme salivary amylase, which begins the breakdown of starch to maltose.

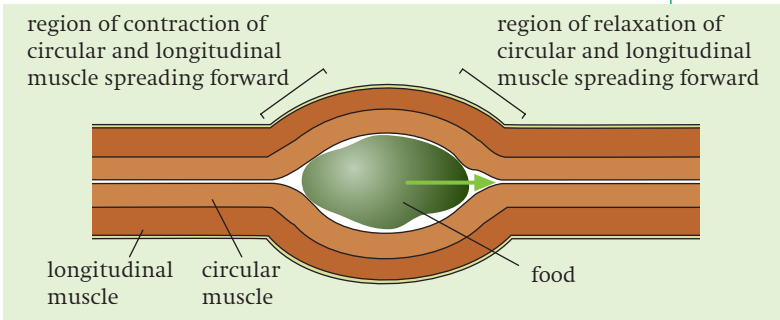
The action of swallowing pushes the bolus into the top of the oesophagus, and a wave of contraction and relaxation takes place along the circular and longitudinal muscles in its walls, pushing the food towards the stomach.

The stomach

The stomach is a sac with a capacity of around 5 dm³. Muscles at each end, known as **sphincters**, control the entry and exit of food to and from the stomach. When a bolus arrives at the stomach from the oesophagus, the upper, **cardiac sphincter**, relaxes to allow the food to enter. The lower,

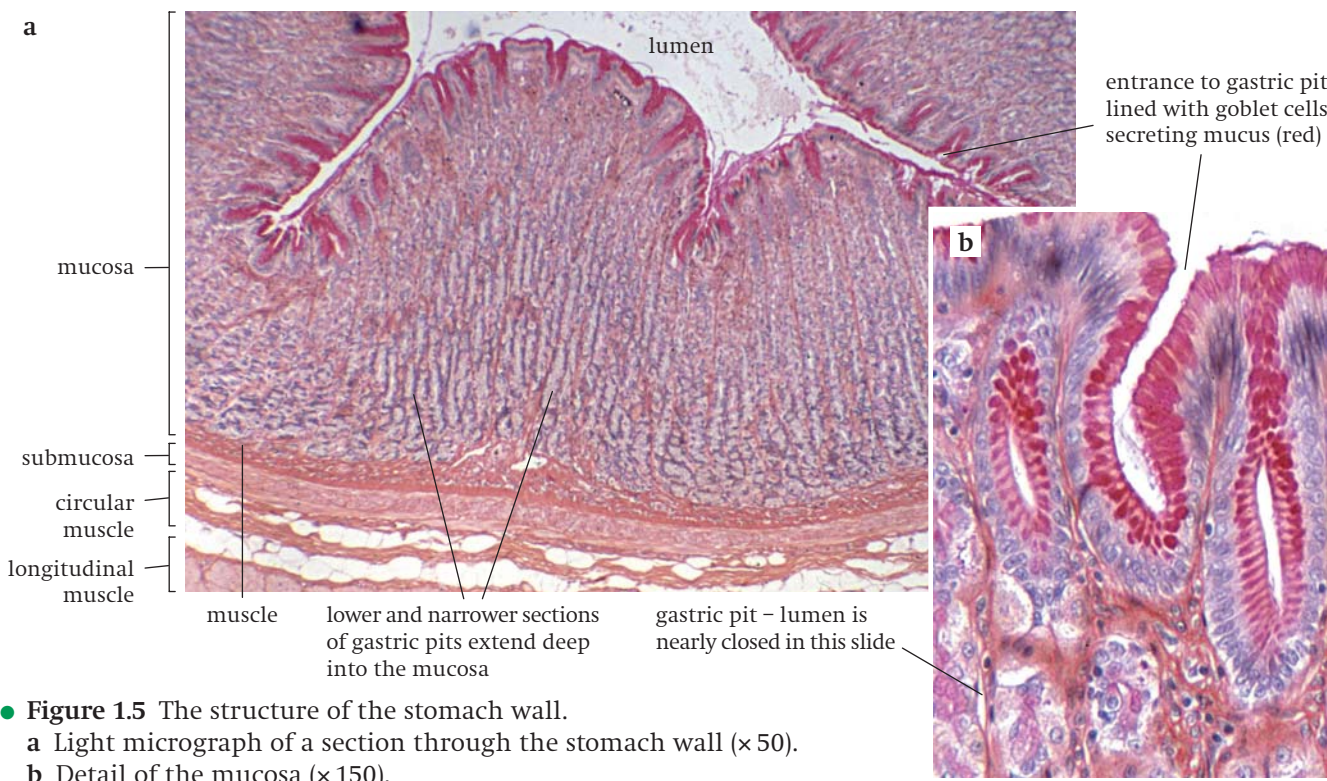
pyloric sphincter, remains contracted so that the food is held in the stomach for up to several hours. It then relaxes to allow the partly digested food, known as **chyme**, to pass into the duodenum.

Figures 1.5 and 1.6 (overleaf) show the structure of the stomach wall. The mucosa is very folded, forming deep pits called **gastric pits** (sometimes called **gastric glands**) which secrete a liquid



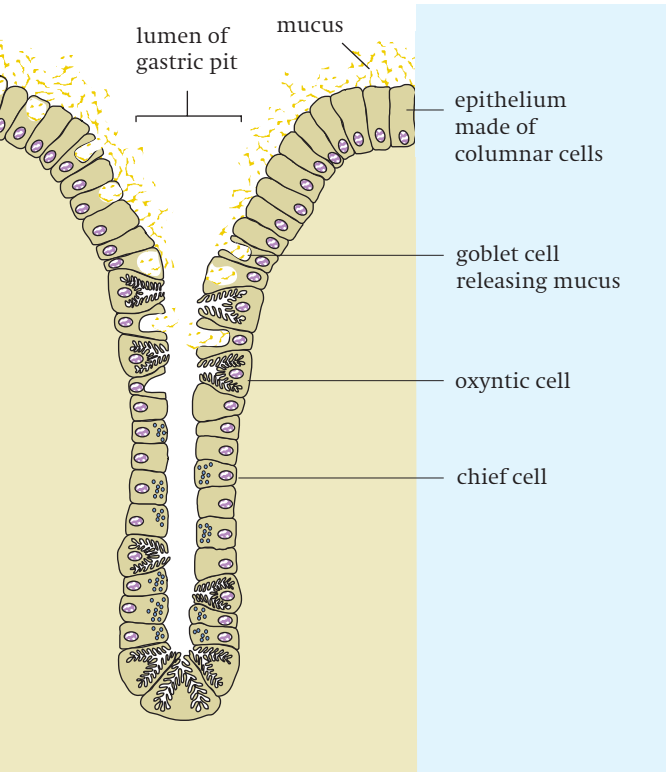
● **Figure 1.4** Peristalsis.

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● **Figure 1.5** The structure of the stomach wall.
a Light micrograph of a section through the stomach wall (× 50).
b Detail of the mucosa (× 150).

known as **gastric juice**. The epithelium of the mucosa (that is the surface layer of cells that make up the stomach wall including the gastric glands) is made up of columnar cells.



● **Figure 1.6** A gastric pit in the stomach wall.

Digestion in the stomach

Gastric juice, like all the fluids secreted into the alimentary canal, is mostly water. It contains **hydrochloric acid**, which is secreted by cells in the epithelium known as **oxyntic** (sometimes called **parietal**) **cells**. These are recognisable by their numerous mitochondria, and the deep invaginations on their surface. This acid gives gastric juice a pH of 1.0 or even less, which is extremely acidic. The acidic environment of the stomach kills a high proportion of the bacteria that may be present in food.

Other cells in the epithelium, known as **chief cells**, secrete a precursor of the protease **pepsin**, known as **pepsinogen**. Pepsinogen does not function as an enzyme, and is converted to active pepsin by the removal of a short length of amino acids from one end of the molecule. This is achieved partly by the hydrochloric acid present in the stomach, and also by pepsin itself.

SAQ 1.1

Suggest why pepsin is secreted in an inactive form.

Gastric juice also contains **lipase**, which begins the breakdown of triglycerides. Both pepsin and

gastric lipase have an optimum pH of well below 7, as they are adapted to function in the acidic conditions of the stomach contents.

The very acidic environment, and the presence of proteases and lipases, present a considerable hazard for the cells of the epithelium of the stomach wall. Protection is provided by the secretion of **alkaline mucus** by goblet cells within the columnar epithelium – so much of it that the whole stomach wall is coated with it. The alkalinity is produced by hydrogencarbonate ions that are secreted along with the mucus.

Absorption in the stomach

The stomach is not adapted for absorption, and none of the major nutrients – carbohydrates, fats or proteins – are absorbed through its walls.

However, there are a few substances that can be absorbed here. They tend to be substances with small, lipid-soluble molecules. One of these is **alcohol**. It can pass through plasma membranes very easily, and some can even be absorbed in the mouth if it is held there long enough. Some medicinal drugs, too, can be absorbed through the stomach wall, including **aspirin**. Unfortunately, taking high doses of aspirin regularly can damage the stomach walls, leading to the development of raw, painful and potentially dangerous ulcers in some people.

The liver and pancreas

The mix of partly-digested food, enzymes and hydrochloric acid passes into the **small intestine** when the pyloric sphincter muscle relaxes. As this happens, juices from two glands – the liver and the pancreas – also flow into the small intestine.

The **liver** is the largest gland in the body. It has many functions, which are described in Chapter 2. One of these functions is the production of **bile**, which is directly concerned with digestion. Bile secreted by the liver is stored in the **gall bladder**, and then carried along the **bile duct** into the duodenum.

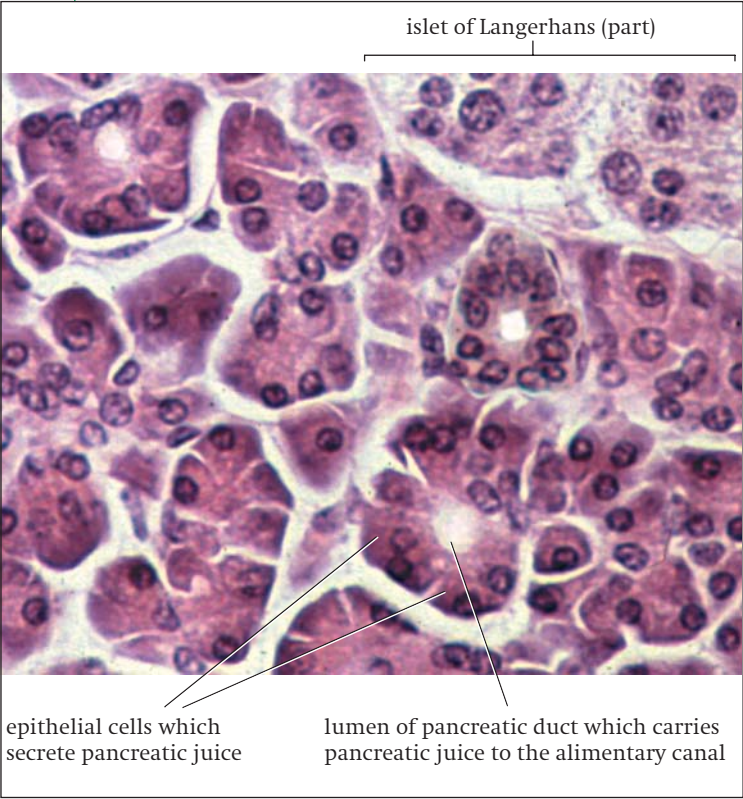
Bile contains several salts derived from cholesterol, including **sodium glycocholate** and **sodium taurocholate**. These salts help

to emulsify fats, breaking fat droplets in the lumen of the small intestine into tiny globules only 0.5 µm to 1.0 µm in diameter. These tiny fat particles disperse into the watery fluids in the intestine. As the food continues on its way along the intestine, a high proportion of the bile salts are absorbed into the blood, eventually finding their way back to the liver. The liver re-secretes them into the bile, and so the cycle continues. One molecule of glycocholate or taurocholate may go round and round like this many times a day.

Bile also contains **hydrogencarbonate ions**, which help to neutralise the acidic mixture of enzymes and partly-digested food entering the duodenum from the stomach.

The **pancreas** is very different in both appearance and function from the liver. Its histology (the structure and arrangement of the tissues within it) is shown in *figure 1.7*.

The pancreas is both an endocrine and exocrine gland. Endocrine glands secrete hormones directly into the blood, while exocrine glands secrete other substances into a duct. The endocrine function of the pancreas is the secretion of the hormones insulin and glucagon (*Biology 2*, page



● Figure 1.7 Light micrograph of pancreatic tissue (× 580).

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101) which control blood glucose levels. This is done by cells in the islets of Langerhans. Its exocrine function is the secretion of **pancreatic juice** into the **pancreatic duct**, which empties into the duodenum.

Pancreatic juice contains a number of enzymes and enzyme precursors. Two proteases, trypsin and chymotrypsin, are secreted in an inactive form, as **trypsinogen** and **chymotrypsinogen**. Trypsinogen will gradually change into trypsin in solution, but this process of activation is speeded up when it comes into contact with another enzyme called **enterokinase**, which is secreted by cells in the wall of the duodenum. Enterokinase removes a short chain of amino acids from the two enzyme precursors, converting them to their active forms. Trypsin can also do this itself, acting on its own precursor, and also the precursor of chymotrypsin, to activate them.

Other enzymes in pancreatic juice include **carboxypeptidase**, **lipase** and **amylase**. Carboxypeptidase is yet another enzyme that is secreted in an inactive form, and is activated when trypsin removes part of its molecule. We will look at the functions of these enzymes in the next section.

Pancreatic juice also contains **hydrogencarbonate ions**. Their function is to neutralise the very acidic mixture of food and gastric juice that flows into the duodenum. All of the enzymes that act in the duodenum and ileum have optimal pHs of neutral or just above.

The small intestine

The small intestine, despite its name, is the longest part of the human alimentary canal, and can be as much as 5 m long. Its name derives from its relatively small diameter compared with other parts of the canal.

The small intestine can be considered to be made up of three different regions – the **duodenum**, **jejunum** and **ileum**. The duodenum makes up the first 25 cm or so of the small intestine, the jejunum the next 2 m or so, and the ileum the remainder. Both the pancreatic duct and the bile duct open into the duodenum.

Figure 1.8 shows the structure of the ileum wall. The most striking feature is the numerous tiny

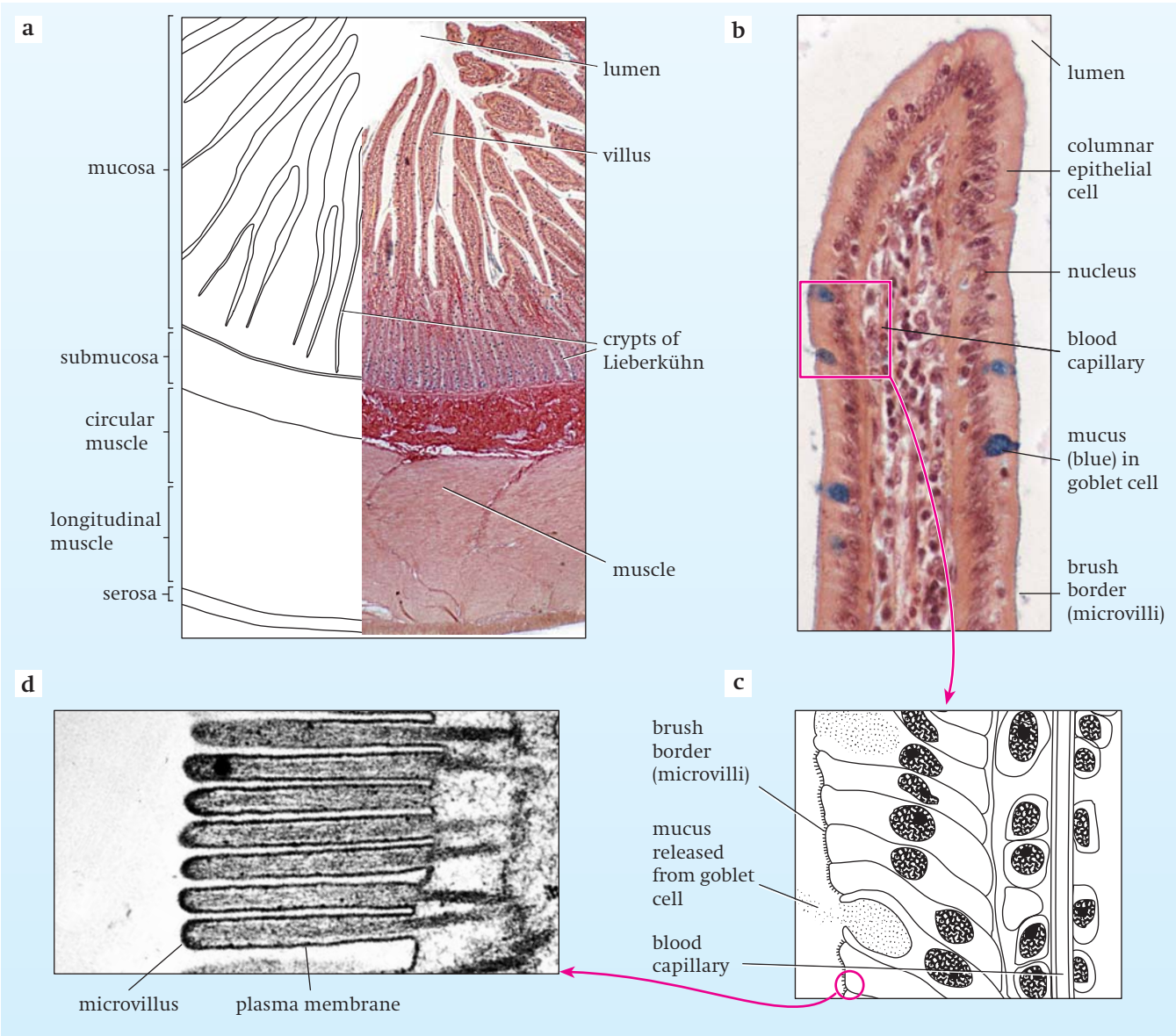
folds, known as **villi**. These are made up of the mucosa layer – that is the epithelium, connective tissue and muscularis mucosa. Each villus is about 1 mm tall, visible with the naked eye, so that if you looked at the inside of the ileum wall it would look rather like velvet. The villi provide an enormous surface area through which, as we shall see, absorption can take place. Each individual epithelium cell on a villus has its own **microvilli**, tiny folds in its surface that increase the surface area even more and that are known as a **brush border**. Each microvillus is about 1 µm long and 0.1 µm wide. The smooth muscle in the muscularis mucosa inside each villus can contract and relax to make the villi sway around, bringing them into good contact with the food in the lumen of the small intestine. Each villus contains a network of blood capillaries, and also a lymphatic capillary, important for the absorption and transport of digested food.

Between the villi are glands known as **crypts of Lieberkühn**. The crypts contain goblet cells that secrete mucus, **Paneth cells** whose function is not known for certain but which may destroy pathogens in the intestine by phagocytosis, and also many undifferentiated cells. These undifferentiated cells divide rapidly, producing new cells to replace old and damaged ones on the surfaces of the villi. In humans, the whole population of cells in the epithelium of the villi is replaced every six days. The newly-produced cells gradually work their way up to the tip of a villus, from where they are shed into the lumen. Presumably their contents can be digested and absorbed into the blood.

Digestion in the small intestine

The various enzymes in the pancreatic juice that flows into the duodenum continue to act on their substrates as the food passes from the duodenum and into the ileum. Protein molecules are hydrolysed first to peptides and then amino acids by trypsin, chymotrypsin and carboxypeptidase, lipids are hydrolysed to fatty acids and glycerol by lipases, and starch is broken down to maltose by amylase.

However, the lumen of the small intestine is by no means the only place where digestion is taking place. Many of the enzymes that act in the ileum do so while actually attached to the surface of the



● **Figure 1.8** The structure of the wall of the ileum. **a** Light micrograph of a transverse section of part of the ileum ($\times 35$). **b** Light micrograph of a longitudinal section through a villus ($\times 520$). **c** Diagram of part of the villus surface. **d** Electron micrograph of the surface of an epithelial cell of a villus, showing microvilli ($\times 70\,000$).

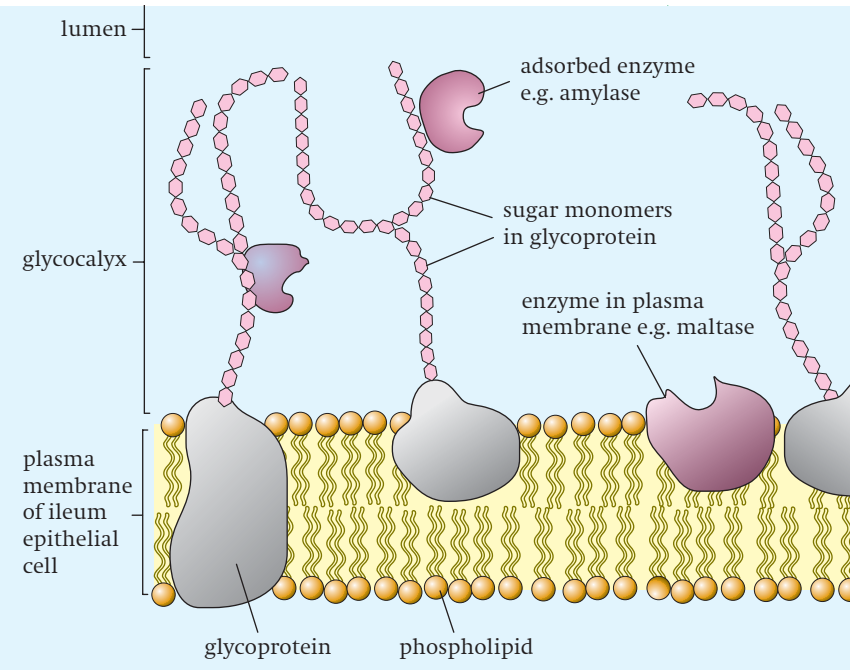
epithelial cells of the villi. Some of the enzymes from pancreatic juice, for example amylase, become adsorbed onto (that is, attached to the surface of) these cells, where they become entangled within the carbohydrate chains of glycoproteins in their plasma membranes (*figure 1.9, overleaf*). This is an efficient way of ensuring that the products of digestion are concentrated right next to the cells that will absorb them.

Another source of enzymes in the ileum is the epithelial cells of the villi themselves. Their plasma membranes contain several different enzymes, held in the membrane with their active sites exposed to the outside of the cell. These enzymes include exopeptidases that produce amino acids from peptides, and carbohydrases such as maltase, that produce monosaccharides from disaccharides. Overall, it appears that only a very small proportion of digestion in the ileum takes place in the lumen – the great majority of it happens right next to the plasma membranes of the epithelial cells.

Absorption in the small intestine

The final products of digestion – amino acids, fatty acids and glycerol, and monosaccharides

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● **Figure 1.9** Digestive enzymes in the ileum. Some of the enzymes from pancreatic juice become trapped within the glycocalyx (the carbohydrate groups of the membrane glycoproteins) of the epithelial cells of the villi. There are also digestive enzymes within the plasma membranes of these cells.

such as glucose – can all cross the plasma membranes of the epithelial cells on the villi, pass right through these cells and enter either the blood capillaries (in the case of amino acids and monosaccharides) or lymphatic capillaries (products of fat digestion). Some of this absorption takes place by diffusion, some by facilitated diffusion, and some by active transport.

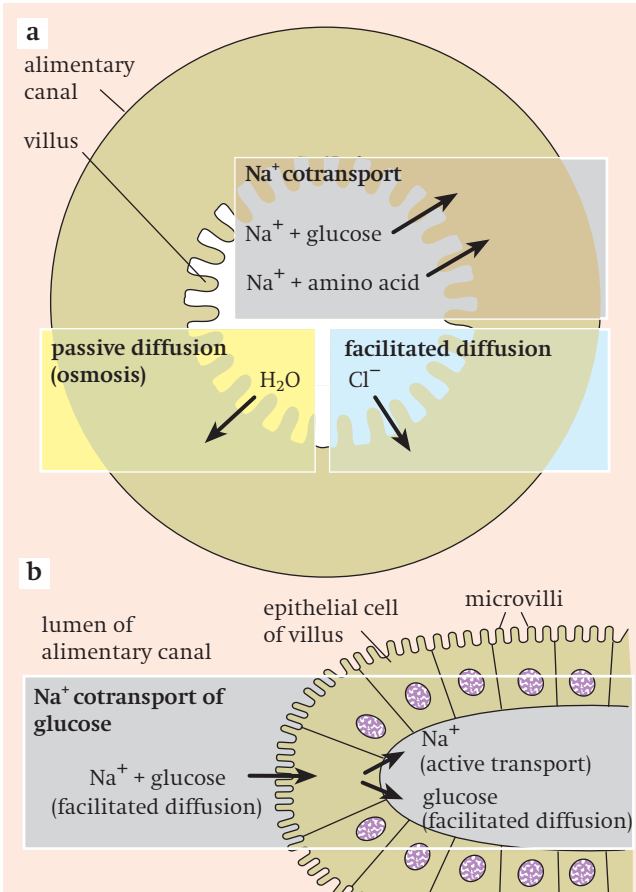
Glucose is mostly absorbed by a type of active transport. Sodium ions are continually pumped out of the base of the epithelial cells into the surrounding tissue fluid, using energy from the breakdown of ATP, against their concentration gradient. As a result, the concentration of sodium ions outside the cells is much greater than inside. Sodium ions from the lumen of the ileum are then allowed to diffuse across the membrane into the cell down their concentration gradient, carrying glucose molecules with them (figure 1.10). This is known as **cotransport**, because the movement of sodium and glucose takes place together.

Amino acids are also absorbed by active transport, mostly by cotransport with sodium ions. In young ruminants (page 14) and rodents,

significant amounts of whole protein molecules can also be absorbed, especially immunoglobulins (*Biology 1*, page 224) present in colostrum – the rich first milk produced by a lactating mother.

Fatty acids and glycerol, being lipid-soluble, are able to diffuse easily through the phospholipid bilayer of the plasma membranes. Once inside an epithelial cell, they are converted back to triglycerides on the smooth endoplasmic reticulum, and then transferred to the Golgi apparatus, where they are surrounded by a protein coat to form a little ball called a **chylomicron**.

(Chylomicrons are a type of lipoprotein, described on page 21.) These then leave the far side of the epithelial cell and enter the lymphatic capillaries. They form a milky emulsion in the



● **Figure 1.10** Absorption in the ileum.
a Summary of the absorption mechanisms for glucose, amino acids, chloride ions and water.
b How sodium–glucose cotransport takes place.