Guts

Second Edition

John Morton

Guts

The Form and Function
of the Digestive System

Second Edition

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General Preface to the Series

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Preface to the Second Edition

Since the first edition in 1967 the study of the gut has advanced on many fronts. These advances were made possible by new physiological methods, such as radio-isotope biology and partition chromatography, and perhaps most of all by the continued use of the electron microscope, an instrument that has given new life and direction to histology. This book has been revised to include a balanced view of what is new, but its old basis has been retained.

One of the merits of the gut system for study is that it is the first and most obtrusive of the great systems a student finds in dissection, and it is a system whose complexity is easy to study. The gut can be studied at a variety of levels from the ecological to the biochemical, and the basic theme of this book is the diversity of gut function at all these levels. Diversity is one of the great themes of biology, and a study of the gut reveals the lavish diversity and design for particular function that is characteristic of all living organisms.

Auckland, 1978   J. E. M.

Contents

1 Introduction: Function and Diversity

1.1 Intracellular digestion

In common with all living organisms animals need a supply of energy. This energy comes from food which must be ingested, taken into the animal, and then prepared for use by the process of digestion. Both ingestion and digestion can occur without a gut. At its simplest ingestion consists of the movement of molecules across a cell or body wall, as happens in protozoans in a culture of dissolved organic material and in some internal parasites. Ingestion can also occur at the cellular level by the process of endocytosis. Pinocytosis (cell drinking) is one kind of endocytosis where droplets of dissolved material are engulfed into a closed vesicle by overarching of the cell membrane, or the pinching off of droplets from tubular invaginations. Within this vesicle cell-wall permeability is lowered and water and solutes diffuse freely into the surrounding cytoplasm. Phagocytosis (cell eating), the other kind of endocytosis, involves the engulfment of particles larger than molecules.

Digestion also varies from one animal to another. In some animals digestion is wholly intracellular; the food passes directly into the cell cytoplasm by phagocytosis and is attacked in food vacuoles by digestive enzymes. More commonly, however, extracellular digestion occurs, although the final stages of digestion may remain intracellular.

The process of intracellular digestion can be observed in the food vacuoles of protozoans. The formation of ingestion vacuoles (phagosomes) in *Amoeba* can readily be followed if Indian ink is added to the food. A certain amount of water is taken in with the food and the vacuoles have at first smooth contours. A minute or so later the vacuoles become invested by granules that stain intensely for acid phosphatase, which is a characteristic of lysosomes. As the ingestion vacuole reduces in size due to loss of water, the lysosomes pour their enzymes into the vacuole which then becomes a digestion vacuole. The amorphous products of digestion gather near the vacuole membrane, which now becomes drawn out into finger-like processes greatly increasing the interface with the cytoplasm, and then move out by 'micro-pinocytosis'. At this stage acid phosphatase cannot be detected and the vacuole becomes simply an egestion vacuole discharging its contents from the cell by exocytosis (Fig. 1–1a).

It is believed that enzymes enclosed in the membranous organelles called lysosomes are present in all cells. Lysosomes are generally identified by the reaction for acid phosphatase, although their enzyme complement includes various carbohydrases (breaking down glycogen and mucopolysaccharides); a range of peptidases (amino-, exo- and
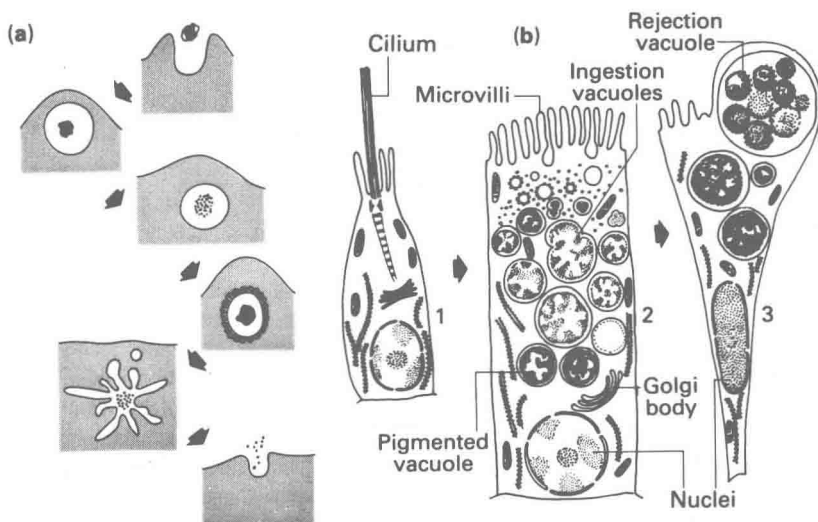
Fig. 1–1 (a) Ingestion and intracellular digestion in the amoeba *Pelomyxa*. (b) Intracellular digestion in the digestive gland of a bivalve mollusc: (1) a young cell in its pre-absorptive stage; (2) a cell during absorption and digestion; (3) a cell during egestion.

endo-peptides), a collagenase, esterases (including acid phosphatase) and nucleases (both RNA-ase and DNA-ase).

The rhizopod protozoans, such as amoeba, are phagotrophic micro-carnivores ingesting other organisms into food vacuoles (Fig. 1–2a). Ciliates are the largest of the protozoans and in many ways foreshadow the complexity of metazoans. The ciliate *Paramecium* has a mouth, the cytostome, at the end of a cytopharynx towards which rows of food-collecting cilia converge. Food particles are impelled through this funnel by ciliary membranelles, enter digestive vacuoles which then pass through a regular cyclic pathway in the endoplasm, and the engested remains are finally expelled from a cytoproct (Fig. 1–2b, c). Carnivorous ciliates, such as *Didinium*, ingest paramecia several times larger than themselves by a cytostome set upon a pointed proboscis.

Intracellular digestion also occurs in the sponges. The flagellate choanocytes, or collar cells, in the inner walls of the sponge not only create water currents which carry food particles into the sponge, but also ingest the food particles. In the simple calcareous sponges the collars of the larger choanocyte cells are made up of microvilli which filter and trap particles which are then passed down the collar by protoplasmic streaming to be phagocytosed at the base. Intracellular digestion is initiated in vacuoles in the choanocytes, but the products are handed on to amoebocytes where digestion is completed and the products transferred throughout the colony (Fig. 1–2d, e).
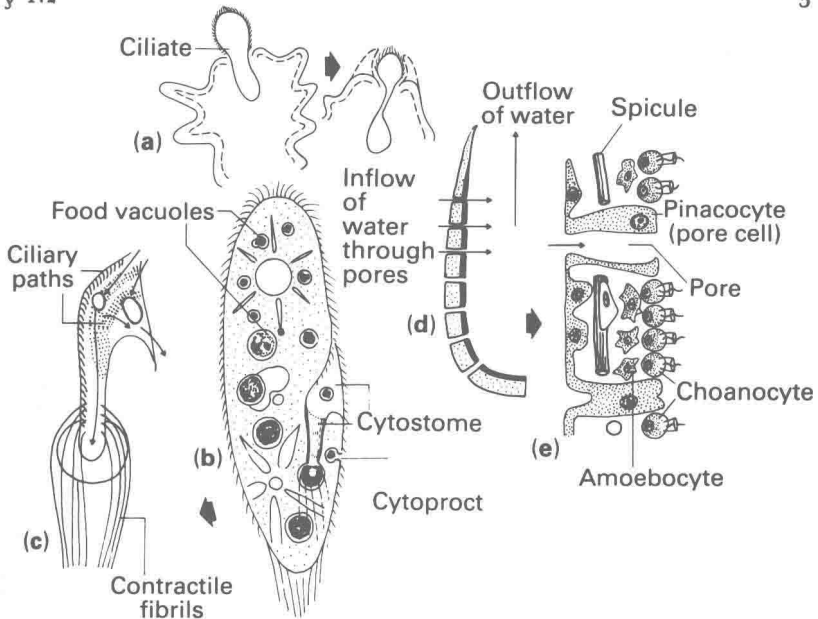
Fig. 1–2 Digestion in protozoans and sponges. (a) Ingestion of a ciliate by *Amoeba*. (b) Pathway of the food vacuoles through the endoplasm of *Paramecium*. (c) Detailed structure of the cytostome of *Paramecium*. (d) Vertical section through the body wall of a simple asconid sponge. (e) Details of the cellular structure of the body wall of an asconid sponge.

1.2   Extracellular digestion

In nearly all metazoan animals there is a permanent gut and so digestion becomes increasingly the work of enzymes secreted into the gut lumen. But in coelenterates, platyhelminthes, nemertines, polyzoans and many molluscs, annelids and echinoderms, the final stages of digestion long remain intracellular. The ultrastructure and activity of the cells of the digestive gland responsible for intracellular digestion in bivalve and gastropod molluscs have received special study. A sequence of stages can be identified, from uptake of particulate food, through digestion and assimilation, to egestion of residual matter into the gut lumen. The first stage is the maturation of small, undifferentiated cells with sparse flagella into mature absorbing cells with a zone of endocytotic vesicles beneath the fringe of microvilli. These vacuoles are converted to phagosomes by the acquisition of lysosomes which lie in the distal half of the cell. The vacuoles show progressive advances in digestion towards the cell base until at the final stage egestion vacuoles remain with unassimilable remains. The cell then rounds off at its free border and releases spherical fragments containing egestion vacuoles. These pass back into the stomach and are eliminated with the faeces. Lysosomes are also discharged in these

fragments, and appear to initiate a new phase of extracellular digestion within the lumen (Fig. 1–1b).

1.3   The construction of the gut

The foods of animals range through virtually everything organic and so may vary enormously in difficulty of procuring and processing. Some foods, like egg yolk and honey, present both pure and highly concentrated nutriment. Some, like blood and milk and coelomic fluid, are nutritious but of inconveniently large volume. Others, such as plankton, require prolonged filtering and concentration, while still others, such as sand, mud and sawdust, are not only heavy and bulky but also very sparse in usable nutrients. The gut will naturally then vary greatly in its adaptations to the nature and bulk of different diets, but a general evolutionary pattern of gut development can be discerned.

In metazoans the different facets of the digestive process have become localized in different parts of the gut and specialized cells are grouped together. Enzymes are liberated to act outside the cell and this extracellular digestion is particularly appropriate for handling large prey. Nevertheless, some simple metazoans rely entirely on intracellular digestion. One of the most primitive flatworms, *Convoluta*, belonging to the order Acoela, has a gut with no internal lumen but a single aperture, the mouth, leading to a solid syncytium, or undifferentiated cell mass (Fig. 1–3b). This can be protruded somewhat like a giant pseudopodium and food is engulfed into vacuoles for intracellular digestion.

The triclad flatworm *Polycelis* also practises intracellular digestion. A long pharynx is inserted into the body of a bulky prey and food material is withdrawn in small fragments to be broken up by muscular contractions of the proboscis and thus prepared for intracellular digestion within the saccular diverticulate intestine (Fig. 1–3c). By contrast, the polyclad flatworm *Cycloporus*, which feeds on zooids of the compound ascidian *Botryllus*, everts a bell-shaped pharynx and sucks out whole zooids. These reach the gut intact, and are broken down entirely within the lumen by extracellular digestion (Fig. 1–3d).

Hydra, an example of the Coelenterata, has a simple gastrovascular or coelenteric cavity lined by gastrodermis (Fig. 1–3a). Water fleas ingested whole are broken down into small particles by extracellular digestion within four hours. Absorptive cells take up these particles into small vacuoles where digestion is completed. These same cells store reserve materials, and dispose of indigestible residues by cell fragmentation.

Although the gut of *Hydra* is simple the cells of the gastrodermis are diversified (Fig. 1–3f). The most numerous are digestive cells which ingest and intracellularly digest food particles. The organelles of these cells are comparable with protozoan food vacuoles and also with the organelles of the molluscan digestive cell (Fig. 1–1b). There are also gland cells of two types. One type secretes mucus to ease the passage of food through the
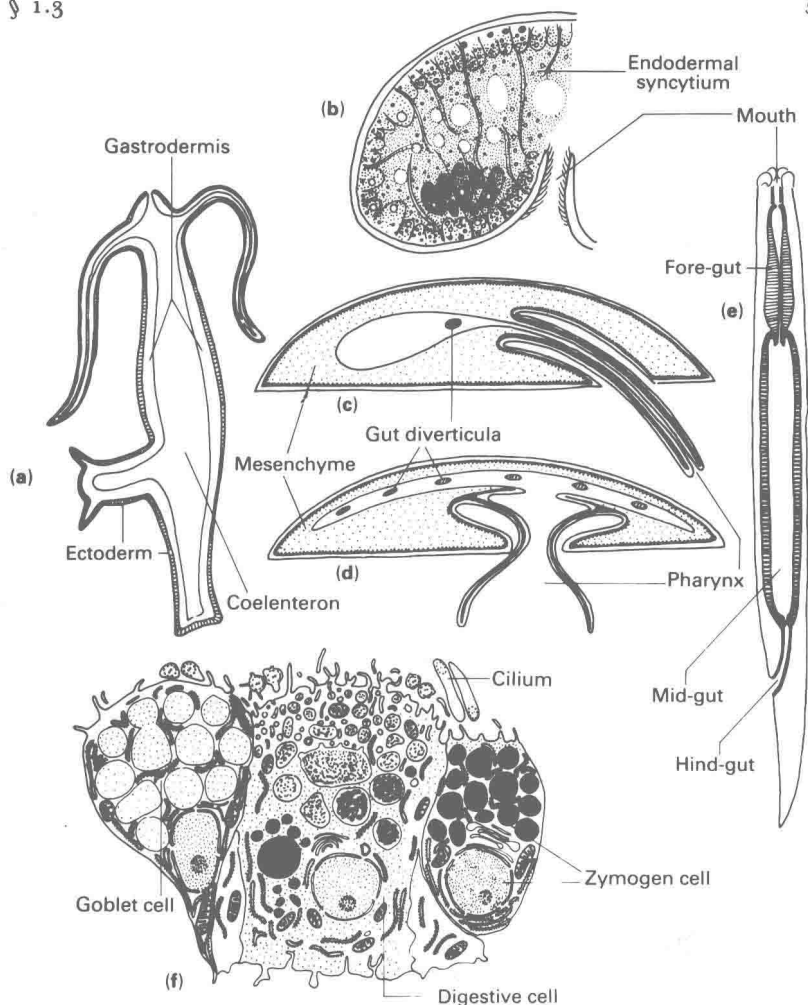
Fig. 1–3 The structure of some primitive digestive systems. (a) *Hydra*. (b) Acoelan flatworm *Convoluta* with a syncytial endoderm. (c) Triclad flatworm *Polycelis*. (d) Polyclad flatworm *Cycloporus*. (e) A simple nematode illustrating gut structure with mouth and anus and the division of the gut into three parts. (f) The three types of cell found in the gastrodermis of *Hydra*.

oral opening and the other, the zymogen cell, releases enzymes for extracellular digestion.

In the Coelenterata and the Platyhelminthes the gut has only a single opening. The next stage in the functional separation of parts of the gut is seen in simple metazoans such as nemertines and pseudocoelomates. A second opening, the anus, is acquired and so the gut takes on the plan of a tube-within-a-tube. The three regions of the gut, fore-gut, mid-gut and

hind-gut, that appeared early in evolution and appear constantly in all later metazoans, can be illustrated by a pseudocoelomate, the nematode (Fig. 1–3e). The fore-gut is a derivative of the embryonic stomodaeum and thus lined with ectoderm. It begins with a buccal or oral cavity, sometimes equipped with jaws or a piercing stylet, and leads through a muscular pharynx to an oesophagus of varying length. No enzymes are produced in the fore-gut, though secretions of the salivary glands released in the buccal cavity may become active here. The mid-gut is derived from endoderm and is a simple tube in nematodes, but it may variously be divided into stomach and intestine, and is the main site of enzyme secretion, digestion and absorption. In molluscs and non-insect arthropods the mid-gut develops a complex mass of diverticula, forming the digestive gland, and other invertebrates such as insects and starfish, have digestive caeca arising from the mid-gut. The hind-gut formed from the proctodaeum, and thus lined with ectoderm, generally has two regions, the colon and the rectum. Its function is to compact and discharge the faeces; in terrestrial animals large amounts of water are reabsorbed here.

Although vertebrates are the most complex metazoans there are close uniformities in gut structure throughout the group. The whole digestive process is now extracellular and except in a few special cases, such as the frog oesophagus, ciliary movement is superseded, and the gut is strongly muscular with rapid peristalsis. Most, but not quite all, vertebrates have a characteristic expanded stomach, separated by a sphincter, the pylorus, from the first part of the small intestine, the duodenum. The stomach constantly changes shape and churns and triturates food to reduce it to a milky chyme.

Peristaltic movements are regular and continuous, under the control of the autonomic nervous system. Peristalsis proceeds by contraction of circular muscle on the oral side and relaxation on the anal side of any stimulated point. Intestinal contents are thus forced towards the anus.

Extracellular digestion is not only rapid but allows division of labour. Different enzymes are produced in sequence by specialized cells, with the pH of the medium adjusted to their working range (Table 1). The vertebrate stomach is defined not by its recognizable form but by the possession of the enzyme pepsin, rarely found among invertebrates. The tubular gastric glands typically have three sorts of cell, goblet cells in the neck of the gland producing mucus, zymogen-type cells secreting pepsin, and parietal or oxyntic cells, distinguished by peculiar intracellular canaliculi, that secrete hydrochloric acid into the lumen (Fig. 1–4a, b, c).

Two organs, both unique to vertebrates, secrete into the duodenum shortly beyond the pylorus. The first, the pancreas, is of composite structure with both exocrine and endocrine portions. The endocrine portion is not directly concerned with digestion, but the exocrine part consists of acini lined with zymogen cells (Fig. 1–4f). These cells are traceable from the early digestive diverticulum of protochordates

(Amphioxus and some tunicates) and some lampreys (Fig. 1–4e) and correspond with the diffuse pancreatic follicles of teleost fish. In the elasmobranchs and all tetrapods, the compound pancreas is a massive gland, opening by a single duct into the duodenum.

Table 1 shows the sources and actions of enzymes including the pancreatic juice and the secretion of intestinal glands known as succus entericus. The pancreas also contributes sodium bicarbonate which reduces the acidity of the chyme received from the stomach.

The second organ, the liver, has many functions but enzyme production is not among them. Its alkaline secretion, the bile, contains bile salts, the breakdown products of haemoglobin, cholesterol and lecithin. The liver's main digestive role is the emulsification of fats by the bile salts, reducing their surface tension so as to break them up into a suspension of fine droplets. The distinctive histology of the liver is shown in Fig. 1–4d, g. Bile is manufactured by columns of cells, bathed by sinusoids, which are the ultimate small blood spaces. Blood passes centripetally through these from the interlobular portal vessels and hepatic arterioles, to the intralobular central vein, which drains back to the hepatic vein. Between the hepatic cells fine bile canaliculi lead centrifugally to the bile ducts.

The liver also has numerous metabolic functions: aminoacids taken up from the portal blood are deaminated, and the resultant —NH_2 converted to urea; absorbed carbohydrates are stored as glycogen; fat is accumulated as such, and metabolized; vitamin A is synthesized from carotene; the special phagocytic cells of Kuppfer remove foreign matter from the blood stream; old red blood cells are removed and, in the foetus, new ones contributed; the blood proteins, prothrombin and fibrinogen, are synthesized; and toxic substances such as alcohol are broken down and rendered harmless.

Intestinal digestion in the mammal leaves a fine milky suspension, chyle, whose contents are ready to be absorbed. The most active site of uptake is the small intestine beyond the duodenum, through the millions of small villi, which constantly contract and expand while bathed with digested food. Both monosaccharides and amino acids pass through the epithelium by active transport, against the diffusion gradient, into the blood plexus inside the villus, to be conducted to the portal circulation. Glucose transport is facilitated by conversion into a phosphate–sugar complex in the absorbing cells. Fats may be taken up by alternate routes: either, after hydrolysis to glycerol and fatty acids, by the portal circulation, or more generally, as a colloidal suspension of whole fat droplets, by the lacteals, which are the axial channels of the villi that lead ultimately to the thoracic duct of the lymphatic system (Fig. 1–4h, i).

The spacious colon has no digestive powers, but its epithelium contains abundant mucous glands. The gut contents remaining after digestion and absorption are concentrated by removal of water. In man, semi-solid faeces are produced after some 36 hours. With normal diet, little
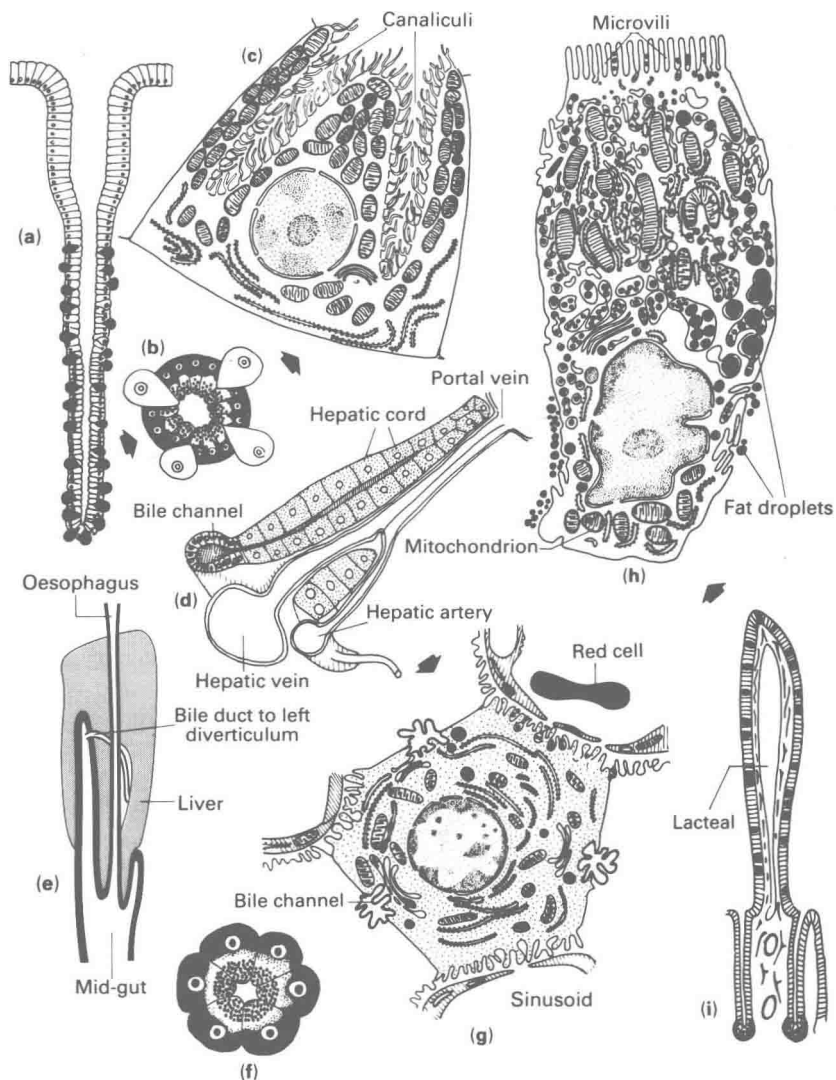
Fig. 1–4 The fine structure of the vertebrate gut. (a) Mammalian gastric tubule showing the gland cells. (b) Cross-section of a mammalian gastric tubule. (c) Oxyntic cell from the mammalian gastric tubule showing the intracellular canaliculi. (d) Cord of hepatic cells and its associated vascular and bile channels. (e) Mid-gut of the larval lamprey showing the relationship between the mid-gut diverticula and the liver. (f) Cross-section of a pancreatic acinus from the teleost fish *Aldrichetta* showing the zymogen exocrine cells. (g) Mammalian liver cell. (h) Fat-absorbing cell of a mammalian villus. (i) Vertical section of a villus showing the lacteal vessel.

Table 1 The sequence of digestive enzymes in the human gut. This enzyme complement is representative of that found in higher animals.

Eaten	Mouth (pH 7)	Stomach (pH 2)	Small intestine (pH 7)	Absorbed
PROTEINS		*pepsin* / *rennin**	*trypsin* (pancreas) / *chymotrypsin* (pancreas) → POLYPEPTIDES	
		POLYPEPTIDES	*carboxypeptidase* (pancreas) / *aminopeptidase* (intestine) → DIPEPTIDES	
			dipeptidase → AMINO ACIDS	AMINO ACIDS
POLYSACCHARIDES	*amylase*		*amylase* (pancreas: intestine)	
DISACCHARIDES			*maltase* / *sucrase* / *lactase* (intestine) → MONOSACCHARIDES	MONOSACCHARIDES
FATS		FATTY ACIDS / GLYCERINE	*lipase* (pancreas: intestine) / *bile salts* (liver)	COLLOIDAL FATS / FATTY ACIDS / GLYCERINE

* Coagulates milk proteins in early life.

undigested or indigestible food remains; faeces continue to be formed during starvation and contain chiefly the residues of bile and other internal secretions, leucocytes, sloughed-off epithelial cells, as well as vast numbers of bacteria, living and dead. They are coloured by stercobilin and other pigments of haemoglobin breakdown from the bile. Their unpleasant odour comes from the compounds indole and skatole, and H_2S, derived from the bacterial breakdown of sulphur-containing amino acids. Bacterial fermentation of carbohydrates also produces CO_2 and methane. The most vital role of the human colon is probably the synthesis of vitamins by its bacterial flora. Colon bacteria invade the infant shortly after birth, and remain important throughout life. Bodily production of the vitamin B complex (riboflavine, nicotinic acid, vitamin B_{12} and vitamin K) is thereafter dependent on the superior synthetic ability retained by these symbionts.

1.4 A functional classification of guts

Although the preceding description reveals a progressive evolution in the complexity of gut structure and function, the remainder of this account will follow a simple functional classification. Lines of division will not follow animal groups but rather the food that animals ingest. Many animals of quite unrelated groups show convergence in the pattern and functions of the gut. This divergence is related to diet and so the lines of division can be made quite simple.

Herbivores and omnivores The gut is here most generalized, with the fullest range of parts. In comparison with carnivores, the food is bulky and may have a large unassimilable component, though it is usually abundant and easy to obtain. The special category of *wood-eaters* is included here.

Deposit feeders Ingesting large quantities of the soft substrate, the food being bulky, diffuse and of low nutritive content.

Carnivores Living on a more concentrated and economic diet, often ingested at long intervals. Food may be of large bulk or small, but it is often hard to catch and there are many specializations for prehension, dismembering and swallowing.

Filter feeders Continuously straining microscopic food from water by cilia and mucous films or screens of setae, often with elaborate devices for concentrating, sorting and transporting the fine food.

Fluid feeders Taking liquids from plants or animals, generally with a piercing and sucking apparatus and some form of muscular pump. The rest of the gut is rather simply constructed, but with ample storage for the fluid meal.

In the following pages a brief survey will be made of each of these five divisions. Numerous examples, even within a single phylum, will be given. This is not profitless repetition, but is necessary to show the essential lesson of the gut which is the flexibility and adaptive resource it displays in nearly every animal group.

2 Herbivores and Omnivores

Though abundant and easy to procure, plant fodder contains stable structural polysaccharides very resistant to digestion. Few animals can by their own enzymes break down the beta-glucose linkages of which cellulose is built up. Instead they rely widely on symbiotic bacteria, ciliates or flagellates.

2.1 Cellulose digestion in ruminants, lagomorphs and macropods

In the ruminant mammals (e.g. cattle, sheep, antelope and deer), bacteria are of primary importance. The stomach and caecum (Fig. 2–1) are storage and fermentation chambers, equipped with a bacterial flora of facultative or obligate anaerobes that attack the food before its contact with digestive enzymes. Ciliate protozoans also live in the ruminant stomach. Bacterial digestion also occurs in the colon, not only in ruminants, but also in the horse and rabbit.

The gut bacteria break down 'difficult' compounds such as cellulose, which are converted in the stomach and elsewhere to volatile and absorbable fatty acids. Acetic acid can be formed *in vitro* by incubating a suspension of cotton wool cellulose with rumen contents at body temperature. Formic, acetic, propionic, butyric, succinic and lactic acids may be produced from various polysaccharides in the rumen and, contrary to popular belief, absorbed there. Blood from the rumen contains a high proportion of these acids, and in the sheep they account for about one quarter of the carbon assimilated from all carbohydrate sources. Carbon dioxide and methane are also produced by fermentation, and are either eructed or eliminated by the lungs. The water milieu and optimum pH in the bacterial chamber are maintained by copious saliva, rich in bicarbonate.

The ciliate protozoans of the rumen seem to play no part in cellulose digestion, although they do digest and assimilate starch. They also feed on the abundant bacteria and ultimately are themselves digested and so provide additional protein for their host. Some gut bacteria can also convert non-protein nitrogen into protein.

The rumen ciliates belong to the order Entodiniomorpha. Two examples are *Entodinium caudatum*, with a circlet of oral cilia and three posterior processes, the largest of which serves as a rudder, and *Epidinium ecaudatum*, with two tufts of immobile cirri at the oral end, and a so-called 'ventral skeletal plate' which is an important store of polysaccharides (Fig. 2–1g).

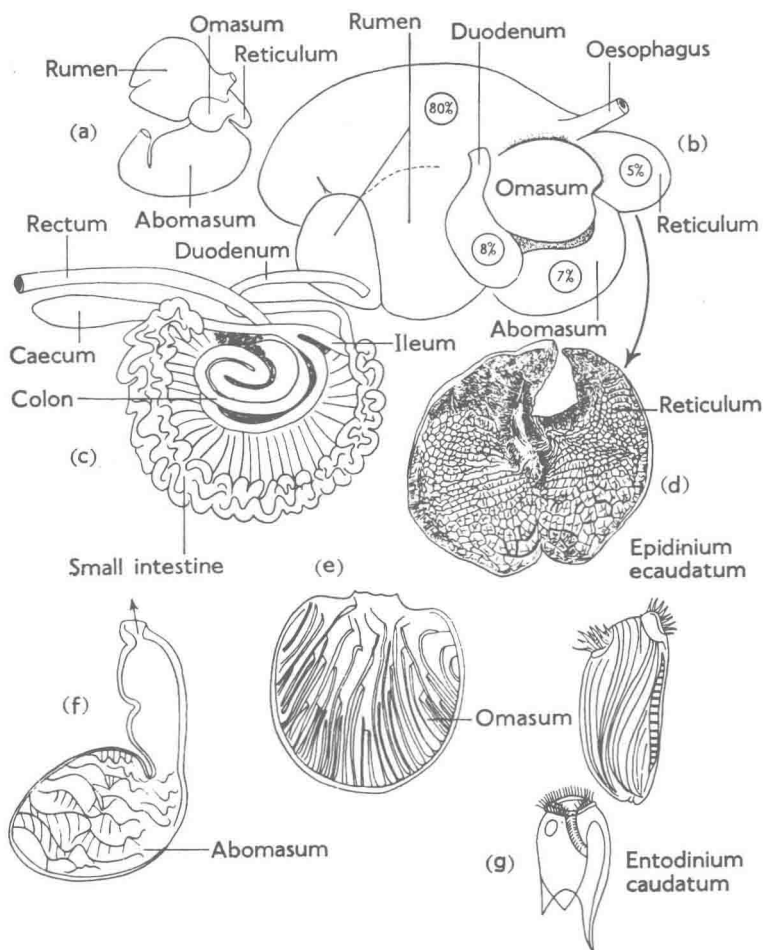The ruminant stomach from the cow is illustrated in Fig. 2–1a, b. Only

Fig. 2–1 The ruminant stomach and its ciliates. (**a**) Stomach of newly-born calf. (**b**) Stomach. (**c**) Intestinal tract of adult ox. (**d–f**) Interior of reticulum, omasum and abomasum. (**g**) *Epidinium* and *Entodinium*.

the true stomach, or abomasum, has peptic glands and it opens straight to the pylorus. In the calf it is larger than all the rest, and provides the milk-coagulating enzyme rennin. The remaining three chambers have a horny lining epithelium and originate as oesophageal sacculations. They are the rumen or paunch; the reticulum or honeycomb (its lining is the source of honeycomb tripe); and the omasum, variously called the manifold, maniplies or psalterium, from its thin page-like folds of epithelium. Although small at birth, the rumen ultimately comes to account for 80% of the total stomach capacity. In feeding, grass passes first from the