

15.1 Structure and function of the gastrointestinal tract

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the gastrointestinal tract Michael E.B. FitzPatrick and Satish Keshav† ESSENTIALS The gastrointestinal tract is a hollow tube stretching from the oral cavity through the oesophagus, stomach, small intestine, colon, and rectum to the anal sphincter. Its function is the transport, digestion, and elimination of ingested material to supply nutrients, vitamins, minerals, and electrolytes that are essential for life, together with the protection of the rest of the body from injurious or allergenic material. The stomach acts as a storage, sterilizing, and digestive tank; the small intestine is the major site of digestion and absorption; the colon's function is to salvage water and electrolytes from the small intestinal effluent; and the rectum provides a storage function, enabling the elimination of colonic residue (defecation) to be restricted to times of personal convenience. Introduction This chapter provides an overview of the anatomy and physiology of the gastrointestinal tract, excluding detail on the liver and pancreas, which are covered elsewhere, and focusing on aspects most relevant to understanding gastrointestinal symptoms and pathophysiology of disease. The prime function of the gastrointestinal tract is to absorb nutrients and water, and omnivorous humans must digest a wide variety of foods, defend against potentially pathogenic microorganisms, and cope with many potentially toxic xenobiotics. Furthermore, the gastrointestinal tract is entirely integrated with other endocrine and neurological systems that are critical for regulating nutrition and metabolism. Anatomical overview The gut is a hollow tube-like viscus extending from mouth to anus, derived from the embryonic endoderm. The pancreas and liver develop as evaginations of the central tube, and remain connected via the pancreaticobiliary duct system. Schematically, the hollow intestinal tract (Fig. 15.1.1) is arranged as an inner layer of absorptive epithelium, underlying lamina propria, smooth muscle muscularis mucosae, loose connective tissue submucosa containing secretory glands, blood vessels, submucosal nerve plexus, and immune cells. Externally is the muscularis externa, generally comprising two layers of

smooth muscle—circular fibres innermost and longitudinal fibres outside. Between the muscle layers is the myenteric nerve plexus, and externally the serosa is covered by a mesothelial epithelial layer. The macroscopic anatomy of the organs comprising the gastrointestinal tract is shown in Fig. 15.1.2. Key features are discussed in the following subsections.

Oesophagus The oesophagus propels a masticated food bolus from mouth and pharynx to the stomach and prevents reflux of stomach content. It is typically 25 cm long, and lies within the posterior mediastinum. It arises at the level of the cricoid cartilage opposite the sixth cervical vertebra and ends at the cardiac orifice of the stomach. It lies posterior to the trachea and thyroid gland in the neck, anterior to the vertebral bodies, with the common carotid arteries and recurrent laryngeal nerves to either side. It passes posterior to the trachea and the left main bronchus at about 28 cm from the incisors, and the left atrium. It passes anterior to the thoracic vertebrae, the thoracic duct, and the azygos vein. The arterial supply is from the inferior thyroid artery, branches of the descending aorta, and the left gastric artery. The venous drainage is via the inferior thyroid veins, the azygos vein, and the left gastric veins. The left gastric and azygos veins form a portosystemic anastomosis at the lower oesophagus, which is where varices typically form in portal hypertension. The oesophagus lacks a serosal layer, lying in a sheath of connective tissue surrounding two muscular layers, an outer layer of longitudinal muscular fibres and an inner layer of circular muscular fibres. These are striated muscle in the superior two-thirds of the oesophagus and involuntary smooth muscle in the inferior third. The oesophagus is lined by a stratified squamous epithelium up to the junction with the gastric cardia, at the so-called z-line. The † It is with great regret that we report that Satish Keshav died on 23 January, 2019.

SECTION 15 Gastroenterologica I disorder 2722 oesophagus contains two functional sphincters, the upper oesophageal sphincter just distal to the pharynx and the lower oesophageal sphincter at the junction with the stomach.

Stomach The stomach can act as a reservoir, accommodating a typical meal, which it homogenizes into liquid chyme adding acid and pepsin to initiate digestion. It is J-shaped (Fig. 15.1.3) and lies below the left dome of the diaphragm, posterior to the left lobe of the liver, anterior to pancreas and kidney, and anteromedial to the spleen. The entire stomach is covered by visceral peritoneum, and it forms the anterior wall of the lesser omental sac, with the greater omentum attached along its lateral, greater curve. The pyloric sphincter opens intermittently to propel chyme into the duodenum. The left gastric artery from the coeliac trunk and the right gastric artery from the hepatic artery supply the lesser curve, while the right gastroepiploic artery from the hepatic artery and the left gastroepiploic artery from the splenic artery supply the greater curve. The vagus nerve supplies efferent and afferent fibres with secretomotor and sensory functions. The gastric muscularis externa is thickened, with a third, inner layer of oblique muscle fibres in addition to longitudinal and circular layers, which contract in a complex, coordinated manner, at a frequency of three times a minute, liquidizing, homogenizing and propelling food.

Small intestine The small bowel is the major site of digestion and absorption. It varies in length between 3 and 10 m and is functionally divided into the duodenum, jejunum, and ileum. The duodenum forms a 25-cm C shape around the head of the pancreas, and is mainly retroperitoneal. The first part distal to the pylorus lies posterior to the liver and anterior to the portal vein and common bile duct. The second part (D2) lies anterior to the right kidney and lateral to the head of the pancreas. The main pancreatic duct enters D2 at the duodenal papilla, surrounded by the muscular sphincter of Oddi, while the accessory pancreatic duct (of Santorini) enters proximally (Fig. 15.1.3). The third part of the duodenum crosses right to left anterior to the aorta and inferior vena cava and posterior to the superior mesenteric vessels, joining the jejunum

at the ligament of Treitz. The jejunum runs into the ileum, and both are highly mobile on a long mesentery attached to the posterior abdominal wall. The whole small bowel distal to D2, as well as the caecum, ascending colon, and transverse colon, is formed from the embryonic midgut and derives its arterial supply from branches of the superior mesenteric artery which are arranged in arcades with considerable collateral circulation. The venous drainage is via the superior mesenteric vein into the hepatic portal vein. The mucosa of the small intestine is distinctive, with multiple adaptations that increase the surface area available for absorption of nutrients: macroscopically, circular folds (plicae circulares) are easily seen. The mucosa itself is arranged in finger-like villi projecting into the lumen, and crypts that penetrate into the lamina propria (Fig. 15.1.1). The villi are lined with a layer of absorptive epithelial cells that themselves are covered on the apical surface by microvilli. Stem cells from which the epithelial cells are constantly and rapidly replenished are situated near the base of the crypts. Other important specialized cells in the epithelium include Paneth cells, which have a role in antimicrobial host defence, goblet cells that secrete mucus, and neuroendocrine cells that produce a variety of enteric (gut) hormones.

Epithelium Mucosa Muscularis mucosae Subserosa Circular muscle Mucosa-associated lymphoid tissue Myenteric plexus Mucosal gland Longitudinal muscle Serosa Enteroendocrine cell Enterocytes (absorptive cell) Goblet cells Progenitor cells Paneth cells Stem cells Intestinal crypt (of Lieberkühn) Villus

Fig. 15.1.1 General arrangement of the layers of the gastrointestinal tract. The high-magnification area shows the villi and crypts of the small intestine.

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Colon The colon absorbs water and electrolytes from the small-bowel effluent to form solid stool for elimination. It is approximately 150 cm in length from the caecum, to which the ileum is attached via the ileocaecal valve, to the rectum, which opens into the anal canal. The appendix vermiformis is attached to the caecal pole. The longitudinal muscle layer is organized into three bands, the taeniae coli, stretching from the appendix to the rectum. The ascending and descending colon are partly retroperitoneal, resting against the posterior abdominal wall, while the transverse and sigmoid colon are peritoneal attached via a mesocolon. The arterial supply to the proximal colon is from the superior mesenteric artery, while the descending colon, sigmoid colon, and rectum, formed from embryonic hindgut, are supplied by the inferior mesenteric artery. The main venous drainage is via the inferior mesenteric vein into the portal circulation.

Rectum and anus The rectum lies in the pelvis anterior to the sacrum and posterior to the vagina or prostate gland and seminal vesicles. It joins the anal canal, lined with a stratified squamous epithelium in its lower half. Defecation is controlled by the two anal sphincters—the internal anal sphincter formed of involuntary smooth muscle and the external anal sphincter formed of striated muscle under voluntary control. The anus receives a dual blood supply from vessels from the inferior mesenteric artery and from the inferior rectal vessels from the internal iliac arteries. The dual venous drainage communicates to form a portosystemic anastomosis.

Physiology Oesophagus The swallowing reflex propels food from the oropharynx into the oesophagus while protecting the airway. This can be initiated voluntarily or by touch receptors in the pharynx. First, the tongue pushes a bolus up and back in the pharynx while the soft palate is pulled upward, preventing the reflux of food into the nasopharynx; then the larynx is elevated against the epiglottis and the vocal cords are pulled together to protect the airway. As the food bolus passes the upper oesophageal sphincter, the sphincter contracts reflexively. This initiates a coordinated, propulsive primary peristaltic wave, controlled by intrinsic neural pathways and the vagus nerve, propagating at 3 to 5 cm/s. Oesophageal distention triggers waves of secondary peristalsis. The lower oesophageal sphincter relaxes at the time of pharyngeal

stimulation and remains relaxed until the bolus enters the stomach (Fig. 15.1.4). Stomach A large number of secretory cells are located in gastric glands. In the fundus and body of the stomach, parietal cells secrete hydro- chloric acid and intrinsic factor, a glycoprotein required for ab- sorption of vitamin B12. Chief cells within the gastric body secrete pepsinogen, which is cleaved to the active protease pepsin by hydrochloric acid. Cells in the neck of gastric glands secrete an al- kaline mucous that protects the gastric mucosa. Endocrine cells in Liver Oesophagus Pancreas Colon Small intestine Caecum Rectum Appendix vermiformis Stomach Gallbladder Fig. 15.1.2 Schematic diagram of the organs of the gastrointestinal tract. Greater curve Lesser curve Pancreas Pylorus Pyloric sphincter Common bile duct Accessory duct of Santorini Duodenum Ampulla of Vater Sphincter of Oddi Incisura angularis Antrum Fundus Cardia Fig. 15.1.3 Structure of the stomach showing cardia, fundus, body, lesser/greater curves, incisura, antrum, and pylorus.

SECTION 15 Gastroenterologica I disorder 2724 the base of the gastric glands secrete somatostatin and gastrin (see 'Hormonal control of gastrointestinal function'). The distensible fundus and body of the stomach create a reser- voir and the muscular distal antrum mechanically disrupts food and mixes it with gastric secretion. Small intestine Chyme entering the small intestine is mixed with pancreatic and biliary digestive secretions, in a process regulated by hormonal and neural mechanisms, responding to intestinal distension, intraluminal nutrients, osmolarity, and pH. Pancreatic secretions in- clude protease precursors, amylase, lipases, and nucleases that hydro- lyse macronutrients to monomers and oligomers that can be absorbed through the brush border of enterocytes via specific transporter pro- teins, generally cotransported with sodium or hydrogen ions. The small intestine has a prodigious capacity to absorb water (Table 15.1.1) driven by active and passive sodium and chloride absorption. The motor patterns of the small intestine are coordinated in both the fasting and fed state (Fig. 15.1.5). After a meal, contractions slowly propel contents along the small bowel allowing time for nu- trient absorption (Table 15.1.2). In the fasted state, coordinated intense contractions ensure that the small intestine is cleared of un- digested residue, preventing microbial overgrowth. Colon The colon absorbs most of the remaining electrolytes and water from the 1 to 2 litres of small intestinal effluent that enters it, leaving approximately 200 ml of faeces to be eliminated daily. The colon also salvages unabsorbed nutrients from the lumen, particularly carbohydrates, which are fermented by the anaerobic bacteria of the colonic microbiota to form short-chain fatty acids, which are then absorbed. Rectum The rectum acts as a reservoir for faeces, allowing periodic defeca- tion. Coordination of the involuntary internal anal sphincter and the voluntary external anal sphincter, as well as the puborectalis Table 15.1.1 Fluid secretion and absorption along the length of the gastrointestinal tract (per day) Location Secretion Absorption Notes Mouth/salivary glands 1500 ml – In addition to approximately 2000 ml fluid ingested/day Stomach 2500 ml – Including hydrochloric acid, pepsinogen, and intrinsic factor Liver/bile 500 ml – Pancreas 1500 ml – Bicarbonate-rich secretions Small bowel – 6000 ml Colon – 1500–2000 ml 200 ml eliminated in stool Pressure topography 0 5 10 Transition Zone Segment 1 UOS S 2 S 3 LOS 15 20 25 30 35 0 5 10 15 20 0 30 60 90 120 150 Pressure (mm Hg) Time (s) Length along oesophagus (cm) Pharynx Upper oesophageal sphincter Upper oesophagus Mid oesophagus Lower oesophagus Lower oesophageal sphincter Fig. 15.1.4 A diagram (left) and high resolution manometry reading (right) of the pressure changes in the pharynx, upper oesophageal sphincter (UOS), oesophagus, lower oesophageal sphincter (LOS), and proximal stomach following a swallow. This shows the primary peristaltic wave (Segment 1) and further segmental pressure events (S2, S3) in the oesophagus, and the sequence of sphincter relaxation. Reproduced from Mainie, I., High resolution manometry and multichannel

intraluminal impedance oesophageal manometry in clinical practice, *Frontline Gastroenterology*, Vol 1 No 2, (2010) with permission from BMJ Publishing Group.

15.1 Structure and function of the gastrointestinal tract 2725 muscle, is required for defecation, passage of flatus, and maintenance of continence. Intestinal fluid balance Table 15.1.1 shows the varying pattern of fluid secretion and absorption along the gastrointestinal tract. Vitamins and minerals are absorbed by various controlled processes in the small bowel. Some, such as vitamin B12, are absorbed in specific locations, with clinical relevance in cases of localized luminal disease or small-bowel resection (see Table 15.1.2). Bile acids exhibit an enterohepatic circulation, first secreted in the bile before being absorbed in the terminal ileum. Regulatory mechanisms The gastrointestinal tract goes through periods of intense activity during meals and relative quiescence afterwards. A variety of neural and hormonal regulatory mechanisms coordinate this. Neural control of gastrointestinal function The gastrointestinal tract has an intrinsic, enteric nervous system controlling several reflexes. There are inputs from the brainstem via the vagus nerve that control the coordinated release of chyme from the stomach and the secretion of bile and pancreatic secretions to optimize digestion. Further reflexes via the prevertebral ganglia integrate contractile patterns and control contractile force in the bowel. Two key reflexes of the gastrointestinal tract coordinated by the enteric nervous system are peristalsis and the migrating motor complex. The peristaltic reflex ensures unidirectional propulsion of luminal contents from mouth to anus. Local luminal distension by a food bolus triggers ascending motor excitation leading to contractions on the oral side of the food bolus while also triggering muscle relaxation distally, generating propulsion. The migrating motor complex is a coordinated contraction of the small bowel during fasting. A period of relative quiescence (phase I) is followed by a period of small, disorganized contractions (phase II). Then larger-amplitude, coordinated contractions propagate down the small intestine. During this phase, the stomach contracts and the pylorus opens fully, allowing residual gastric and small-bowel contents to be flushed into the colon. This cycle repeats every 90 minutes unless a meal is consumed (Fig. 15.1.5). There are further neural interactions between the central and enteric nervous systems which are poorly understood. This brain-gut axis is thought to play a key role in a range of functional bowel disorders, such as irritable bowel syndrome and visceral hypersensitivity, and may well explain some of the gastrointestinal manifestations of psychological conditions, such as anxiety and depression. Hormonal control of gastrointestinal function Several hormones regulate gastrointestinal tract function, and the most important are shown in Table 15.1.3. These are released from enteroendocrine cells in the gastric mucosa, which sense changes in luminal contents and exert local paracrine, as well as more distant hormonal, effects. Immunological function of the gastrointestinal tract The gastrointestinal tract is a major site of contact with the external environment and the range of potentially pathogenic viruses, bacteria, protozoa, fungi, and helminths that could be ingested with food. The gut's physical barriers include a thick mucus layer, the mechanical effect of secretion and peristalsis, and tight junctions between epithelial cells, while gastric acid, alkaline intestinal secretions, bile acids, and high concentrations of digestive enzymes create a chemically hostile environment for microorganisms. In addition, intestinal epithelial cells, including highly specialized cells such as Table 15.1.2

Absorption of key vitamins and minerals within the gastrointestinal tract

Vitamin/mineral	Site of absorption	Relevant information
Iron	Duodenum	Absorbed via divalent metal transporter protein, DMT1, transported basally via ferroportin
Vitamin B12	Terminal ileum	Absorbed bound to intrinsic factor secreted in the stomach
Folate	Jejunum	
Vitamins A, D, E, K	Duodenum, jejunum, ileum	Fat-soluble vitamins
Calcium	Jejunum	Calcium lost in bile reabsorbed by small

intestine. Calcium bound to phytates cannot be absorbed D1 D2 J1 J2 J3 30 min. Fig. 15.1.5 Peristalsis and the migrating motor complex (MMC): the MMC demonstrated in manometry readings from the duodenum (D1/2) and jejunum (J1–3) showing two phase III contractions propagating down the gastrointestinal tract (marked with dotted lines). The quiescent phase I and small-amplitude contractions of phase II can be seen between them. Reprinted by permission from Springer Nature: Soffer EE, Thongsawat S, Ellerbroek S (1998) Prolonged ambulatory duodeno-jejunal manometry in humans: normal values and gender effect. *Am J Gastro*, 93, 1318–23, copyright © 1998.

SECTION 15 Gastroenterologica I disorder 2726 Paneth cells and goblet cells, secrete antimicrobial peptides and enzymes such as defensins and lysozyme (Fig. 15.1.6). The intestinal wall also contains many immune cells, arranged within gut-associated lymphoid tissues (GALTs), and distributed in the lamina propria and the epithelial layer. GALT includes lymphoid follicles and Peyer's patches that lie just below the epithelial layer, which contains specialized M-cells that allow transepithelial transport of luminal antigens. Plasma cells within the lamina propria secrete dimeric immunoglobulin A, which is transported into the lumen of the intestine by active secretion by epithelial cells, and has a role in regulating the composition of the intestinal microbiota. Although various mechanisms limit the survival of microorganisms, many do survive, and the intestinal lumen, particularly in the colon, contains a large population of commensal bacteria, including enterococci, clostridial species, Proteobacteria, and bifidobacteria. The role of this resident microbiota in health and disease is increasingly recognized, with complex interactions between specific bacteria and the innate and adaptive immune system. In, for instance, inflammatory bowel disease, certain strains are more frequently found in the diseased intestine, and the overall diversity of bacterial species appears to be reduced. In a number of experimental models, transplantation of the microbiota has been shown to transfer complex traits, such as obesity and immune activity. This has led, in some cases, to attempts to treat disease through modification of the microbiome by prebiotics, probiotics, and faecal microbial transplantation. This suggests that when we consider the structure and function of the intestine, the microbial content, which includes approximately 10^{13} bacterial cells, could be considered an intrinsic component of this organ system. FURTHER READING Ellis H, Mahadevan V (2013). *Clinical anatomy: applied anatomy for students and junior doctors*, 13th edition. Wiley Blackwell, Chichester. Hollister EB, Chunxu G, Versalovic J (2014). Compositional and functional features of the gastrointestinal microbiome and their effects on human health. *Gastroenterology*, 146, 1449–58. Honda K, Littman DR (2016). The microbiota in adaptive immune homeostasis and disease. *Nature*, 535, 75–84. Koepfen B, Stanton B (eds) (2017). *Berne & Levy physiology*, 7th edition. Elsevier, Philadelphia, PA. Standing S (ed) (2016). *Gray's anatomy: the anatomical basis of clinical practice*, 41st edition. Churchill Livingstone, Edinburgh.

Hormone	Source	Stimulus for release	Targets	Effect	
Gastrin	G cells (gastric antrum)	Oligopeptides in gastric lumen	Gastrin-releasing peptide from enteric neurons	Parietal cells of stomach (directly and via histamine release from enterochromaffin-like (ECL) cells)	Stimulates acid secretion from parietal cells
Cholecystokinin (CCK)	I cells (duodenum)	Fatty acids, protein	Vagal afferent terminals	Pancreatic acinar cells	Inhibits gastric emptying and acid secretion Stimulates pancreatic enzyme secretion and gallbladder contraction
Secretin	S cells (duodenum)	Low (acidic) luminal pH	Pancreatic duct cells	Stimulates pancreatic duct secretion	
Peptide YY	L cells (terminal ileum and colon)	Fatty acids, protein	Enteric nervous system neurons in the stomach and small bowel	Inhibits	

gastric emptying and reduces intestinal motility Somatostatin Delta cells (gastric antrum) Low (acidic) luminal pH G cells of stomach Reduces gastrin secretion leading to reduced parietal cell acid secretion Glucagon-like peptide-1 (GLP-1) L cells (small intestine) Fatty acids, glucose Neurons, epithelial cells Glucose homeostasis Enteroendocrine cell Enterocytes (absorptive cell) Goblet cells Progenitor cells Paneth cells Stem cells Intestinal crypt (of Lieberkühn) Villus

Fig. 15.1.6 The intestinal crypt and its cell types: Paneth cells and stem cells are located at the base of the intestinal crypts (of Lieberkühn). Absorptive enterocytes line the top of the crypts and form the majority of the cells of the villous mucosa interspersed with goblet cells and enteroendocrine cells, with progenitor cells in the middle of the crypts in between.

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