Varastegan
Institute for Medical Sciences

Digestion, Absorption, Transport, and Excretion of Nutrients

(Session 6)

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Digestion and Absorption of Specific Types of Nutrients

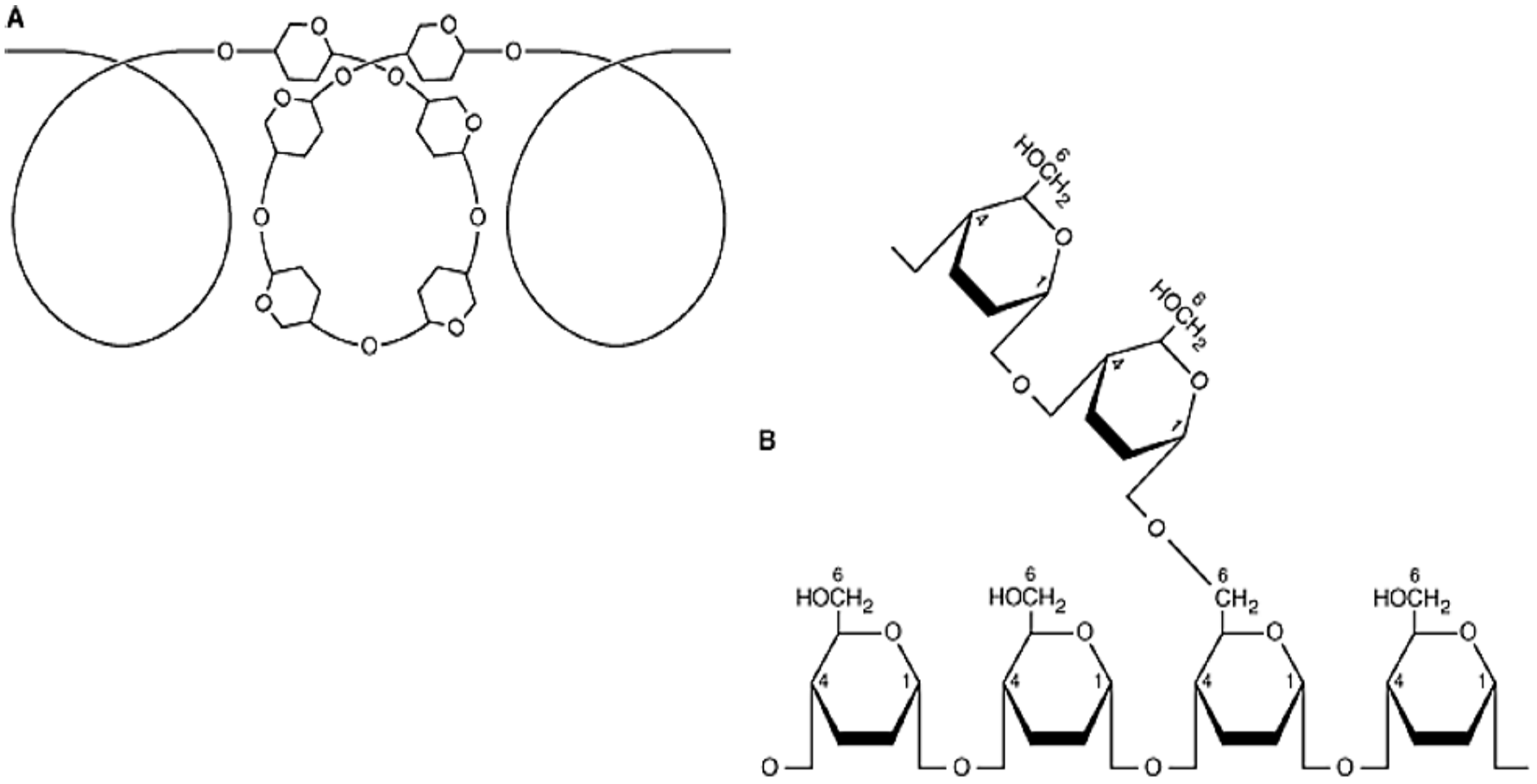
Carbohydrates and Fiber

Most dietary carbohydrates are consumed in the form of starches, disaccharides, and monosaccharides.

Starches, or polysaccharides, usually make up the greatest proportion of carbohydrates.

Starches are large molecules composed of straight or branched chains of sugar molecules that are joined together, primarily in α-1-4 or α-1-6 linkages.

Most of the dietary starches are amylopectins, the branching polysaccharides, and amylose, the straight chain-type polymers.



Structure of starch: (A) Amylose, showing helical coil structure; (B) Amylopectin, showing 1→6 branch point

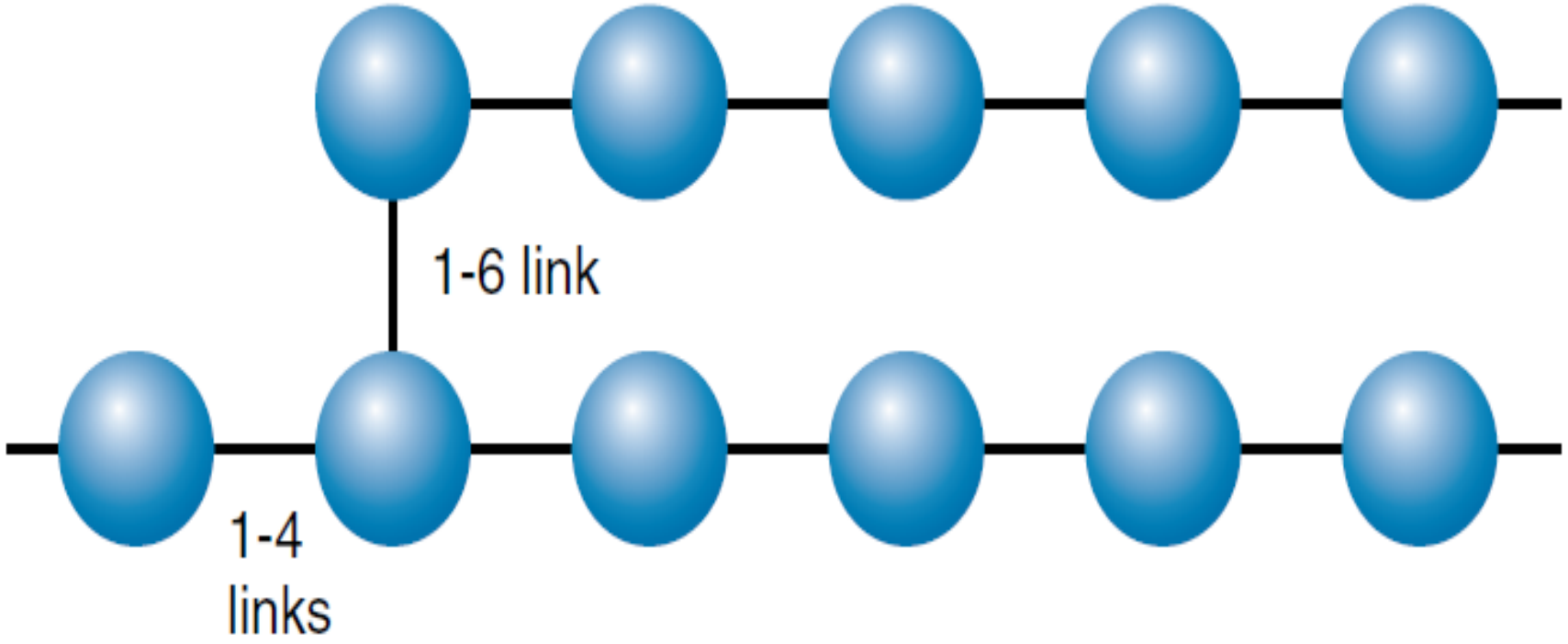
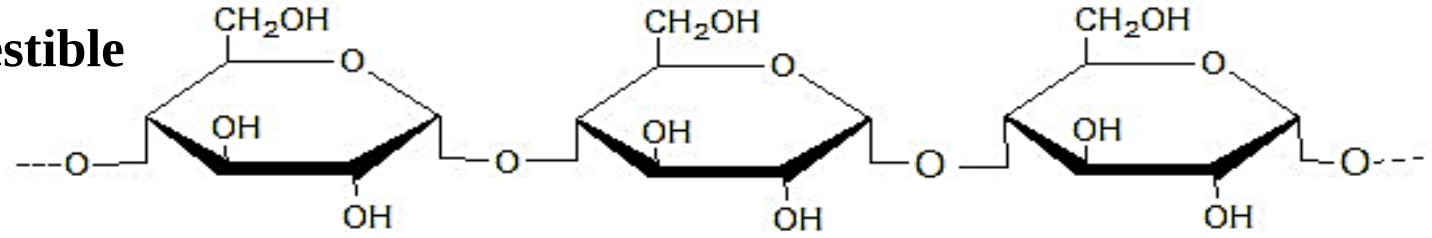


Fig. 2.2. Starch is composed of amylose (15% to 20%) and amylopectin (80% to 85%). Amylose is a nonbranching helical chain structure of glucose residues, whereas amylopectin (a portion shown here) has branched chains of 24 to 30 glucose residues *(blue)* joined by *(1→4)* glucosidic linkages with *(1–6)* linkages creating the branching points.

Dietary fiber is also largely made of chains and branches of sugar molecules, but in this case the hydrogens are positioned on the beta (opposite) side of the oxygen in the link instead of the alpha side, resulting in its resistance to enzymatic digestion in human GIT.

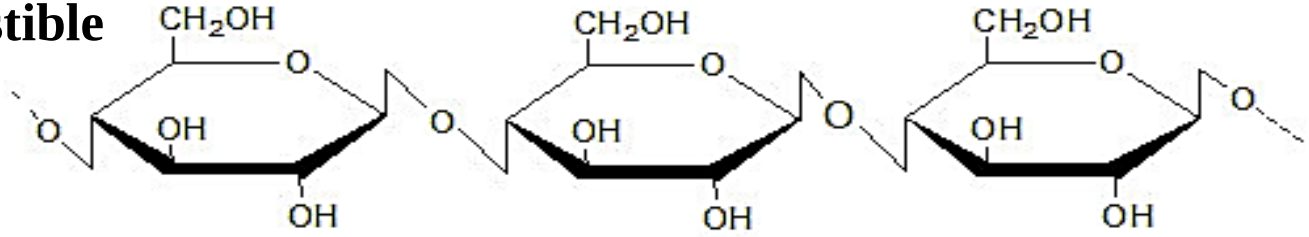
That humans have significant ability to digest starch, but not most fiber, exemplifies the "stereospecificity" of enzymes.

Digestible



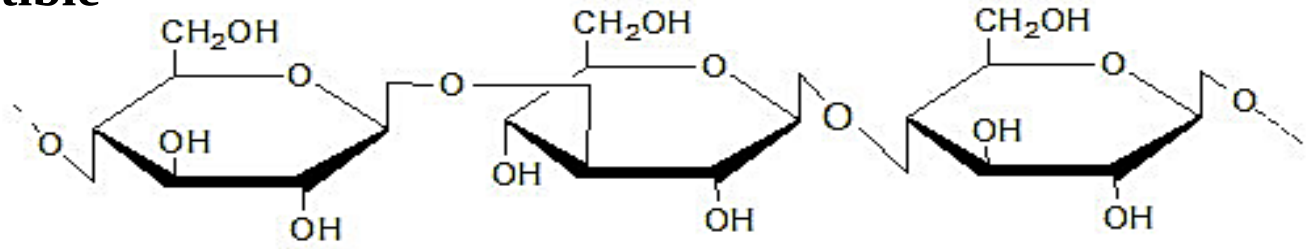
Amylose: α-1,4 glucosidic bonds

Indigestible



Cellulose: β-1,4 glucosidic bonds

Indigestible



β-Glucan: mixed β-1,3 and β-1,4 glucosidic bonds

In the mouth, salivary amylase (ptyalin) operates at a neutral/slightly alkaline pH and hydrolyzes a small amount of the starch molecules into smaller fragments, and then becomes deactivated after contact with HCl.

The stomach empties before significant carbohydrate digestion can take place; thus, most carbohydrate digestion occurs in the proximal small intestine.

Pancreatic amylase breaks the large starch molecules at α-1-4 linkages to create maltose, maltotriose, and "alpha-limit" dextrins remaining from the amylopectin branches.

Enzymes from the brush border of the enterocytes further break the disaccharides and oligosaccharides into monosaccharides glucose, galactose, and fructose.

The brush border of the enterocytes contain the enzymes maltase, sucrase, lactase, and isomaltase (or a-dextrinase), which act on maltose, sucrose, lactose, and isomaltose, respectively.

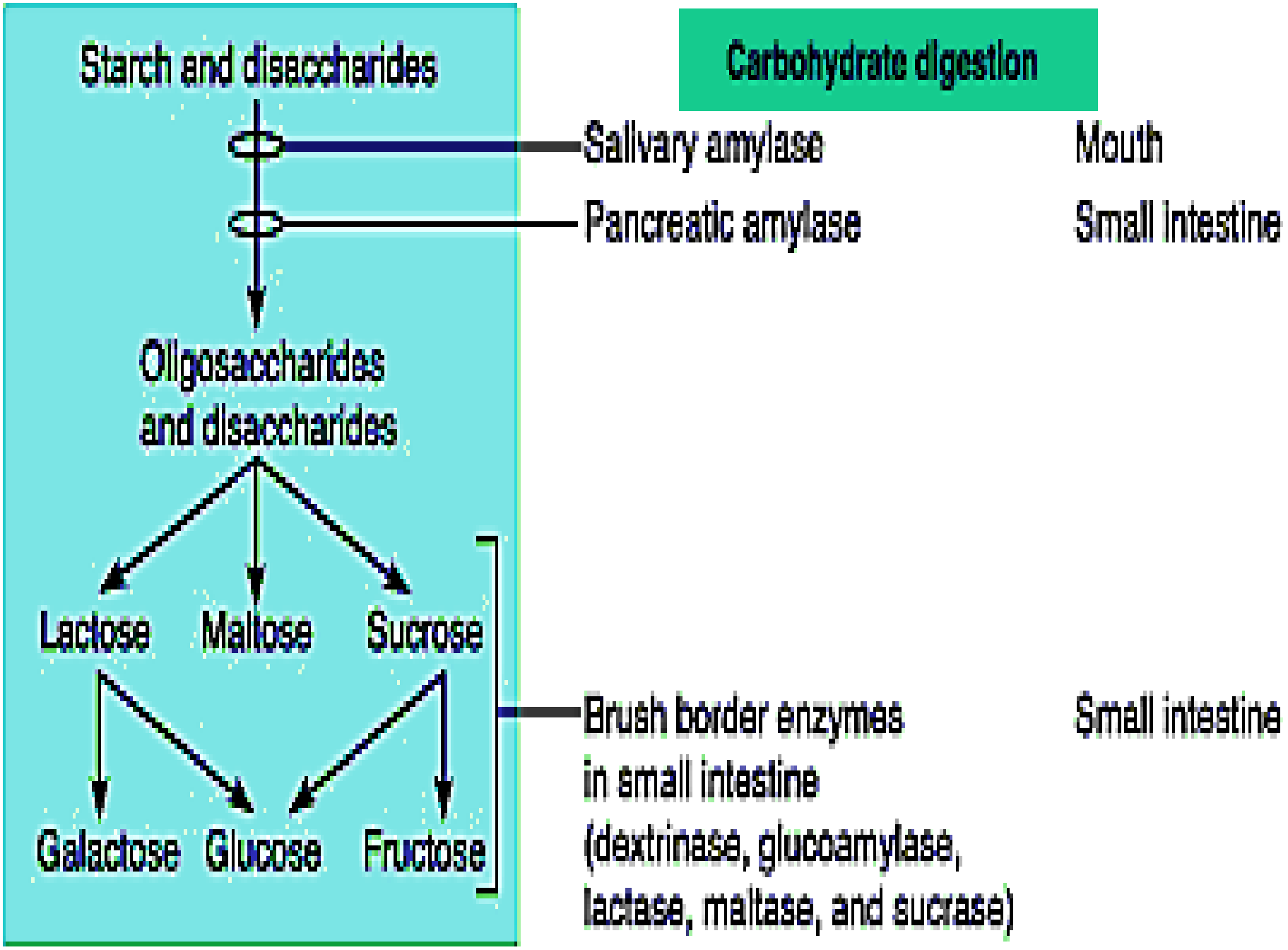
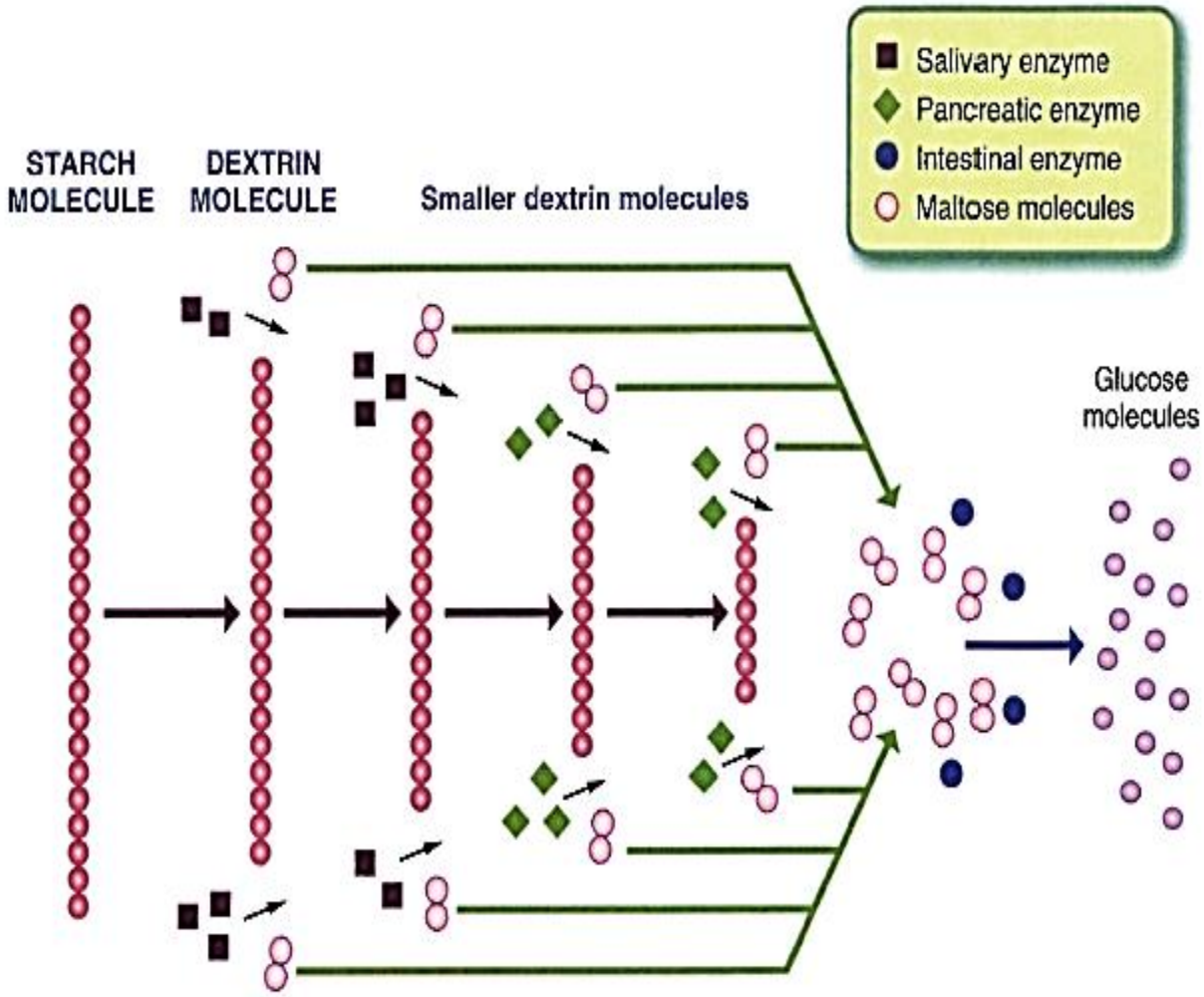

Carbohydrate digestion
Starch and disaccharides
Salivary amylase
Mouth
Pancreatic amylase
Small intestine
Oligosaccharides
and disaccharides
Lactose
Maltose
Sucrose
Galactose
Glucose
Fructose
Brush border enzymes
in small intestine
(dextrinase, glucoamylase,
lactase, maltase, and sucrase)
Small intestine

FIGURE 1-7 The gradual breakdown of large starch molecules into glucose by digestion enzymes.



Glucose, galactose, and fructose pass through the mucosal cells and into the bloodstream via the capillaries of the villi, where they **are carried by the portal vein to the liver**.

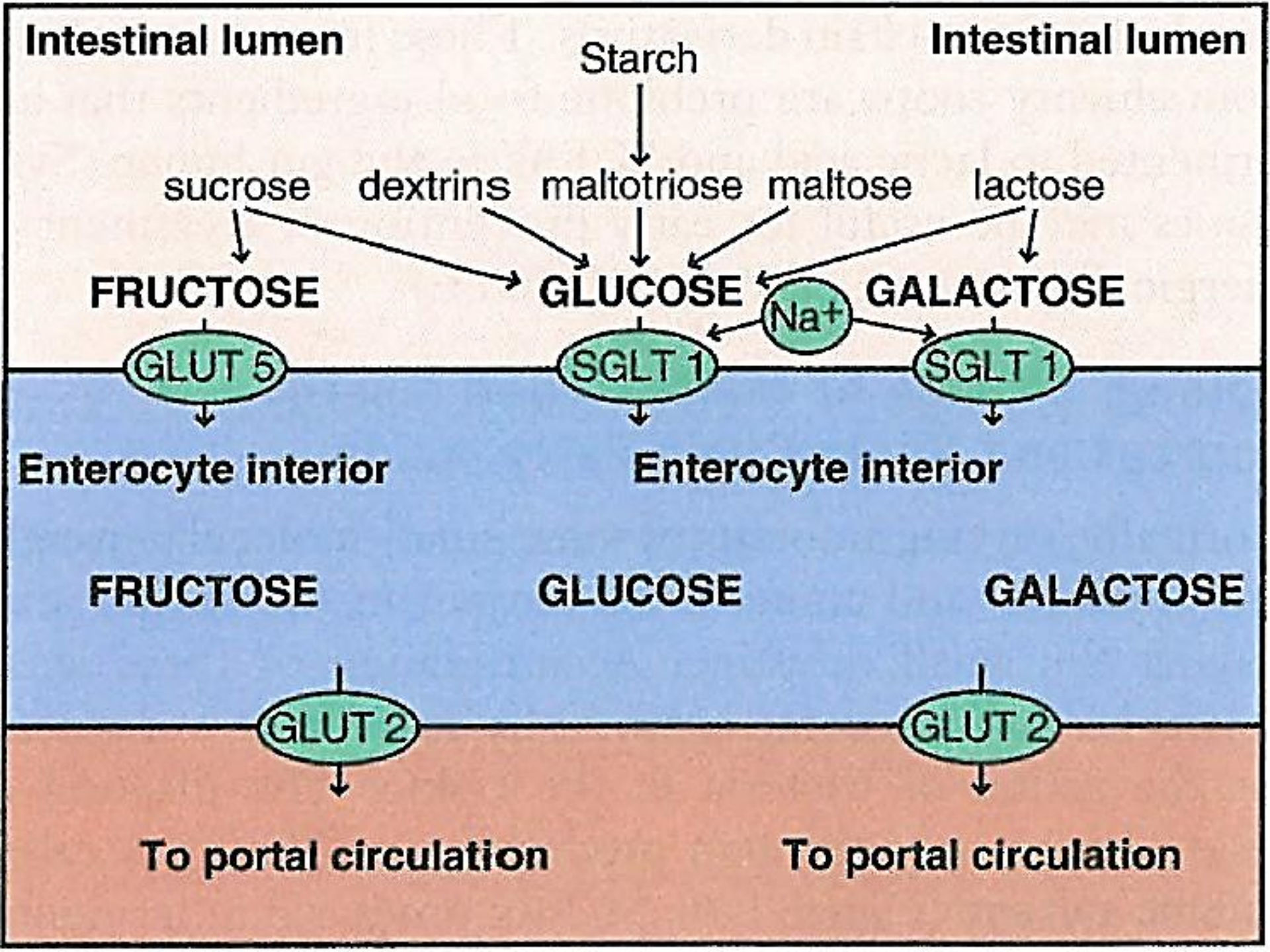
At low concentrations, glucose and galactose are absorbed by active transport, primarily by a sodium -dependent transporter called the glucose (galactose) cotransporter.

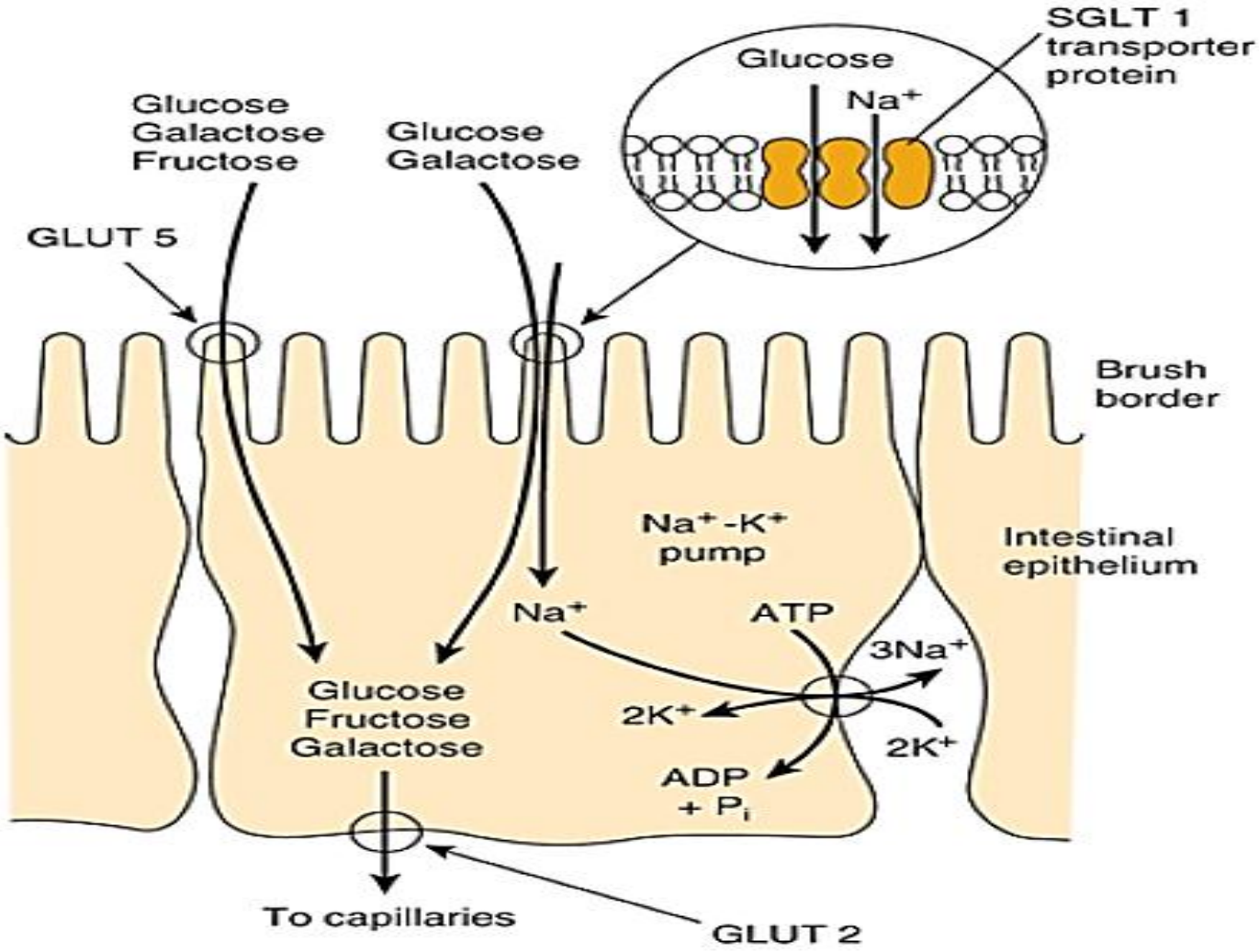
At higher luminal concentrations of glucose, glucose transporter (GLUT) 2 becomes a primary facilitative transporter into the intestinal cell.

Fructose is more slowly absorbed and uses GLUT5 and the facilitative transporter from the lumen.

GLUT2 is used to transport glucose, galactose, and fructose across the intestinal cell membranes into the blood.

The sodium-dependent transport of monosaccharides is the reason why sodium-glucose drinks are used to rehydrate infants with diarrhea or athletes who have lost too much fluid.


Intestinal lumen
Starch
Intestinal lumen
sucrose
dextrins
maltotriose
maltose
lactose
FRUCTOSE
GLUCOSE
GALACTOSE
Na+
GLUT 5
SGLT 1
SGLT 1
Enterocyte interior
Enterocyte interior
FRUCTOSE
GLUCOSE
GALACTOSE
GLUT 2
GLUT 2
To portal circulation
To portal circulation



Transport of glucose, fructose, and galactose across the intestinal epithelium. The SGLT 1 transporter is coupled to the Na^+ - K^+ pump, allowing glucose and galactose to be transported against their concentration gradients. The GLUT 5 Na^+ - independent facilitative transporter allows fructose, as well as glucose and galactose, to be transported down their concentration gradients. Exit from the cell for all sugars is via the GLUT 2 facilitative transporter.

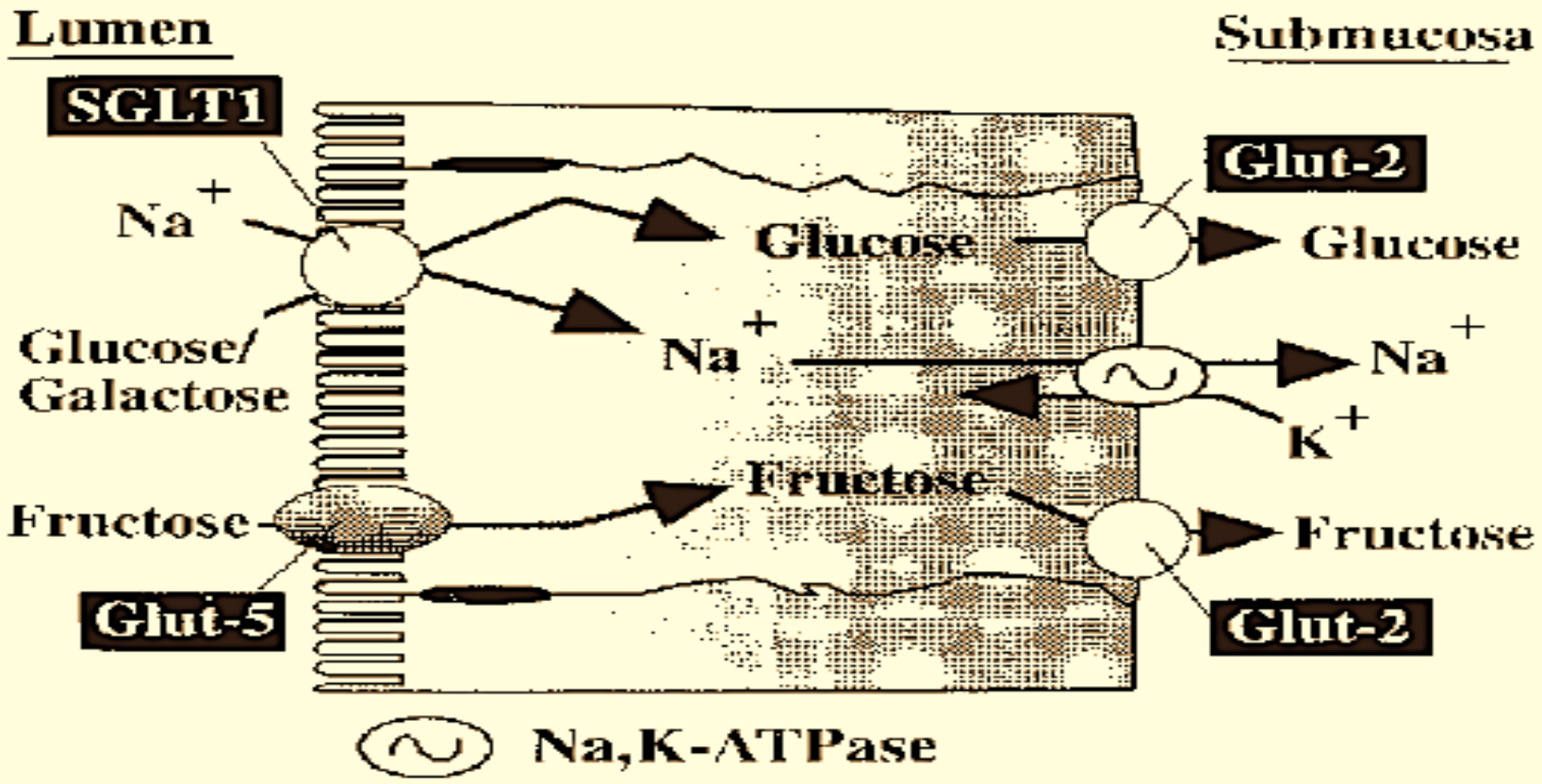


Fig. 42.15. Monosaccharide absorption by the enterocyte occurs by active and passive processes. Glucose and galactose are absorbed by a sodium (Na)-dependent glucose/galactose transporter (SGLT1), driven by an Na^+ gradient generated by Na^+/potassium (K^+)/adenosine triphosphatase (ATPase) at the basolateral membrane of the enterocyte. Fructose is absorbed by facilitated diffusion using a glucose transporter called GLUT5. All monosaccharides exit the enterocyte by facilitated diffusion via a carrier protein called GLUT2. (Reprinted with permission from Chang EB, Sitrin MD, Black DD, eds. Gastrointestinal, Hepatobiliary, and Nutritional Physiology. Philadelphia: Lippincott-Raven, 1996:125.)

TABLE 2.4 HUMAN FACILITATED-DIFFUSION GLUCOSE TRANSPORTER FAMILY (GLUT1 TO GLUT5)

TYPE	AMINO ACIDS (N)	CHROMOSOME LOCATION	K_m (mmol/L) FOR HEXOSE UPTAKE[a]	MAJOR EXPRESSION SITES
GLUT1 (red cell)	492	1	1–2 (red blood cells)	Placenta, brain, kidney, colon
GLUT2 (liver)	524	3	15–20 (hepatocytes)	Liver, β cell, kidney, small intestine
GLUT3 (brain)	496	12	10 (*Xenopus* oocytes)	Brain, testis
GLUT4 (muscle/fat)	509	17	5 (adipocytes)	Skeletal and heart muscle, brown and white fat
GLUT5 (small intestine)	501	1	6–11(fructose) (*Xenopus* oocytes)	Small intestine, sperm

K_m, Michaelis-Menten constant.

[a]The approximate K_m values refer to the uptake of glucose (fructose in the case of GLUT5) in the designated tissue or cells in parentheses and are shown to give an approximate index of the affinity of the transporter for glucose.

Consumption of large amounts of lactose (especially in individuals with a lactase deficiency), fructose, stachyose, raffinose, or alcohol sugars (e.g. sorbitol, mannitol, or xylitol) can result in considerable amounts of these sugars passing unabsorbed into the colon and may cause increased gas and loose stools.

Cellulose, hemicellulose, pectin, gum, and other forms of fiber cannot be digested by humans; thus these carbohydrates pass relatively unchanged into the colon, where they are partially fermented by bacteria in the colon.

Other resistant starches and sugars are also less well digested or absorbed by humans, but are fermented into SCFAs and gases.

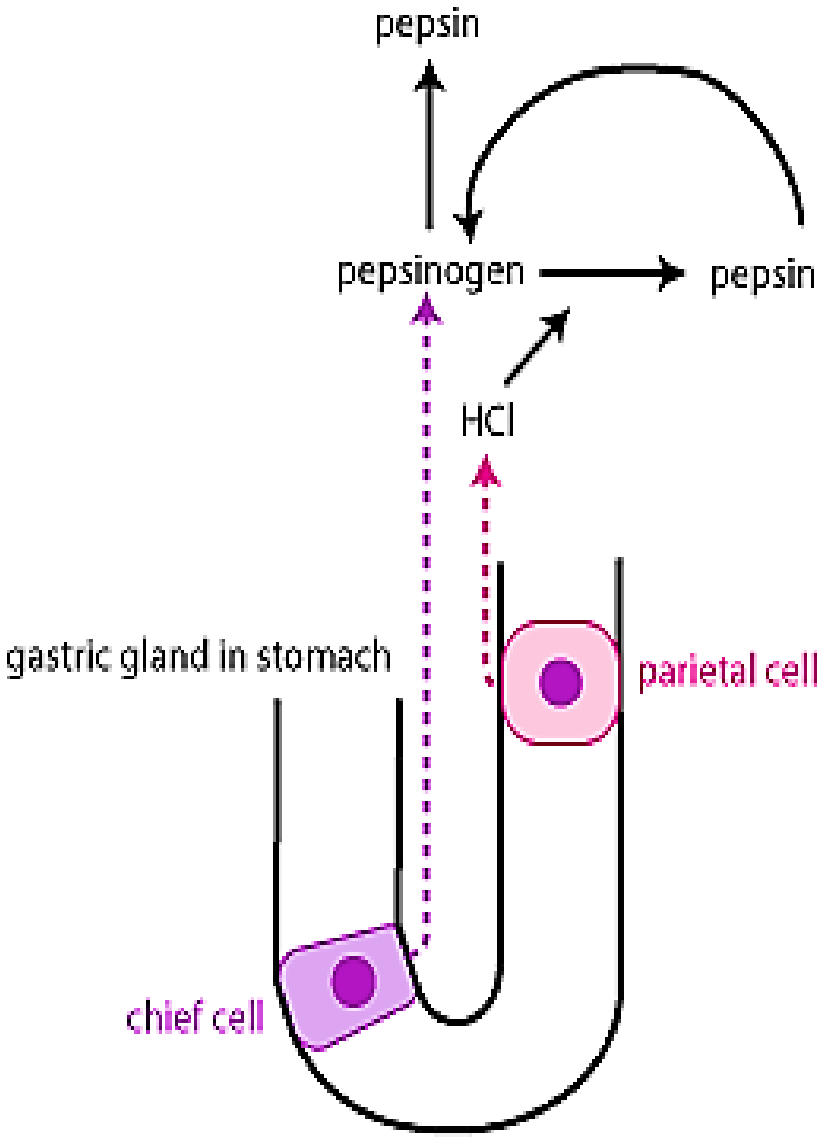
It is noteworthy that one form of dietary fiber, lignin, is made of cyclopentane units and is neither readily soluble nor fermentable.

Proteins

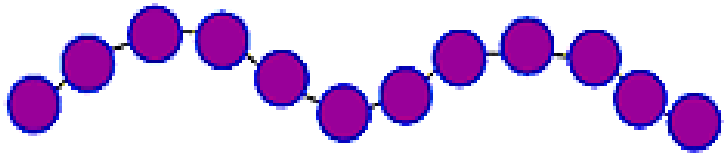
Protein digestion begins in the stomach, where some of the proteins are split into polypeptides by the enzyme pepsin.

Inactive pepsinogen is converted into the enzyme pepsin when it contacts HCl and other pepsin molecules.

Unlike any of the other proteolytic enzymes, pepsin digests collagen, the major protein of connective tissue.

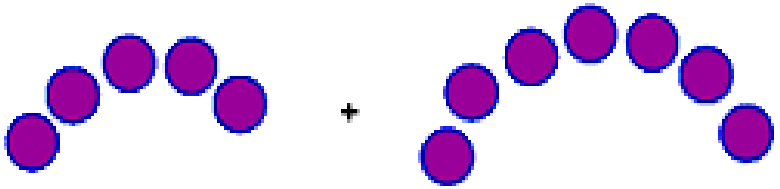


Digestion of protein / polypeptide



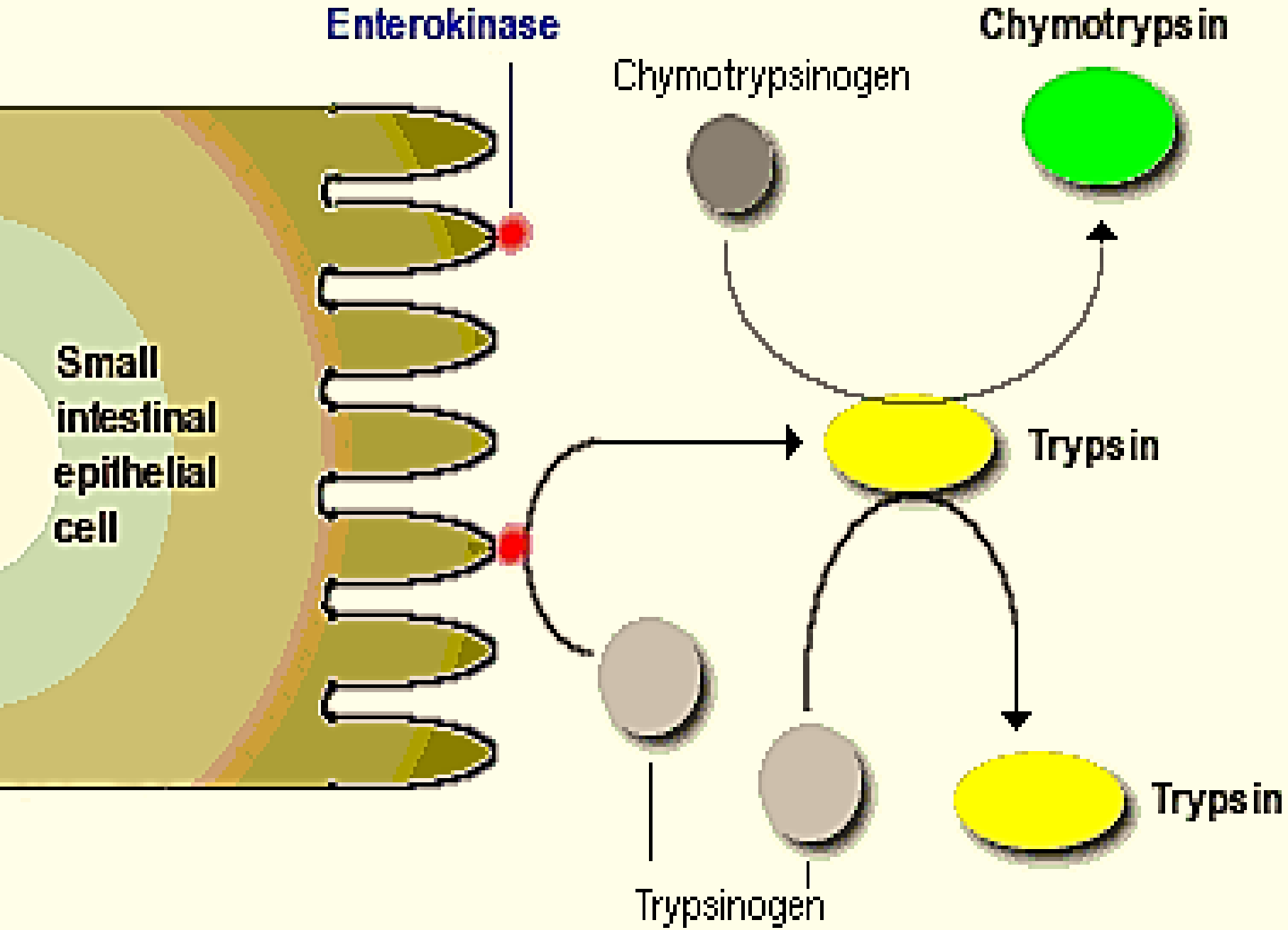
The peptide bonds between the amino acids are hydrolysed

Pepsin is a protease that hydrolyses the protein into smaller polypeptides



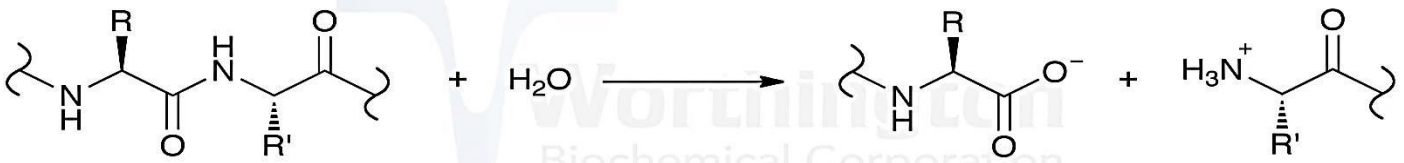
Contact between chyme and the intestinal mucosa stimulates the release of enterokinase, an enzyme that transforms inactive pancreatic trypsinogen into active trypsin (i.e. the major pancreatic protein-digesting enzyme).

Trypsin in turn activates the other pancreatic proteolytic enzymes.


Enterokinase
Chymotrypsin
Chymotrypsinogen
Small intestinal epithelial cell
Trypsin
Trypsin
Trypsinogen

Pancreatic trypsin, chymotrypsin, and carboxypeptidase break down intact protein to small polypeptides and amino acids.

Trypsin



Polypeptide

Polypeptide fragments

R = Arg and Lys

Chymotrypsin

Polypeptide

Polypeptide fragments

R = Phe, Trp, and Tyr; R' ≠ Pro

Carboxypeptidase

Polypeptide (**n** residues)

Polypeptide (**n-1** residues)

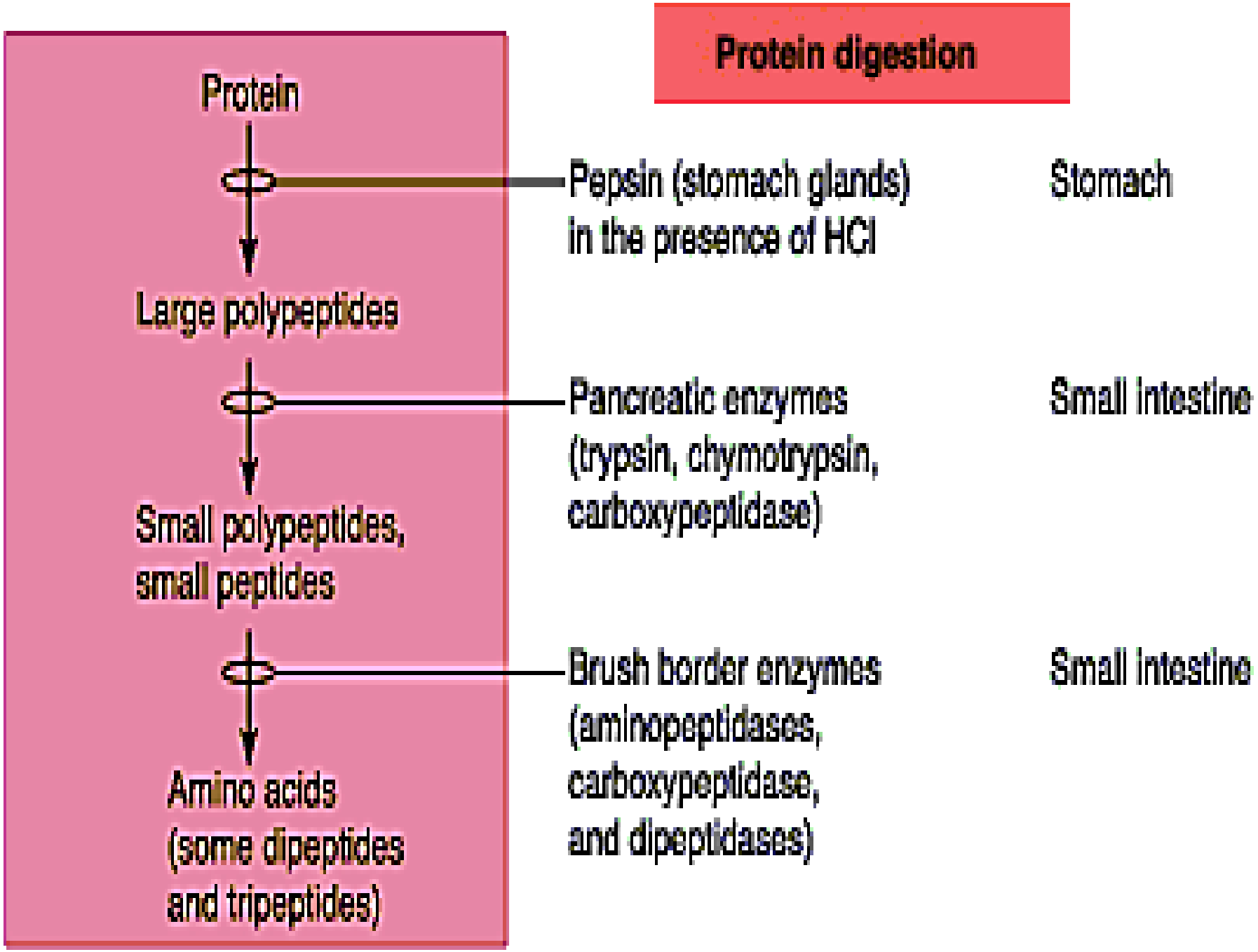
Amino Acid

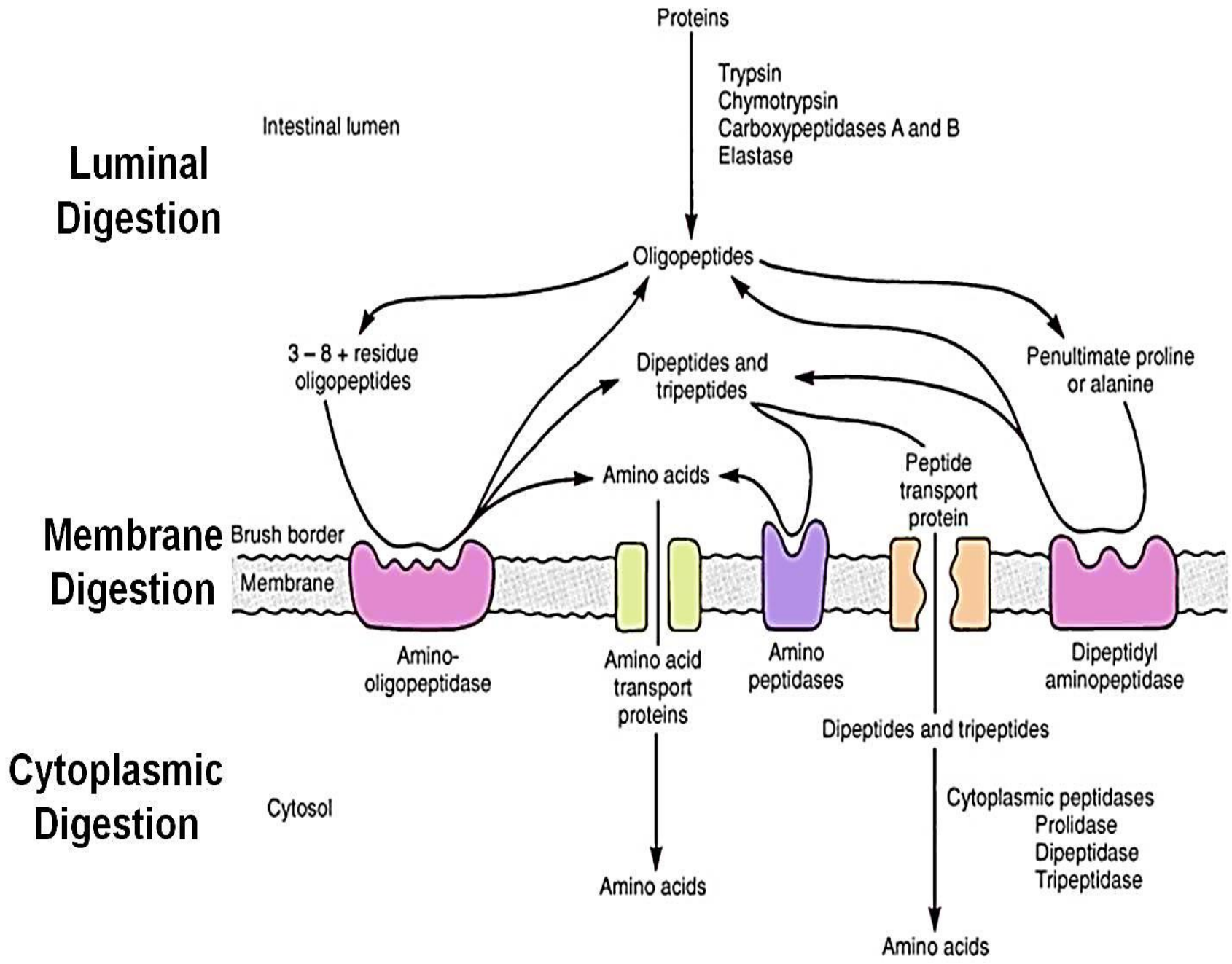
R' = Arg, Lys, and ornithine

Proteolytic peptidases located on the brush border also act on polypeptides, breaking them down into amino acids, dipeptides, and tripeptides.

The final phase of protein digestion takes place in the brush border, where some of the dipeptides and tripeptides are hydrolyzed into amino acids by peptide hydrolases.

End products of protein digestion are absorbed as both amino acids and small peptides.


Protein digestion
Protein
Pepsin (stomach glands) in the presence of HCl
Stomach
Large polypeptides
Pancreatic enzymes (trypsin, chymotrypsin, carboxypeptidase)
Small intestine
Small polypeptides, small peptides
Brush border enzymes (aminopeptidases, carboxypeptidase, and dipeptidases)
Small intestine
Amino acids (some dipeptides and tripeptides)


Proteins
Trypsin
Chymotrypsin
Carboxypeptidases A and B
Elastase
Intestinal lumen
Luminal Digestion
Oligopeptides
3 – 8 + residue oligopeptides
Dipeptides and tripeptides
Penultimate proline or alanine
Amino acids
Peptide transport protein
Membrane Digestion
Brush border
Membrane
Amino-oligopeptidase
Amino acid transport proteins
Amino peptidases
Dipeptidyl aminopeptidase
Dipeptides and tripeptides
Cytoplasmic Digestion
Cytosol
Cytoplasmic peptidases
Prolidase
Dipeptidase
Tripeptidase
Amino acids
Amino acids

Several transport molecules (sodium- or chloride-dependent, etc.) are required for the absorption of amino acids, probably because of the wide differences in the size, polarity, and configuration of the different amino acids.

Considerable amounts of dipeptides and tripeptides are also absorbed into intestinal cells using a peptide transporter, a form of active transport.

TABLE 1.5 AMINO ACID TRANSPORTERS

SYSTEM	AMINO ACID TRANSPORTED	TISSUE LOCATION	pH DEPENDENCE
Sodium dependent			
A	Most neutrals (Ala, Ser)	Ubiquitous	Yes
ASC	Most neutrals	Ubiquitous	No
B	Most neutrals	Intestinal brush border	Yes
N	Gln, Asn, His	Hepatocytes	Yes
N^m	Gln, Asn	Muscle	No
Gly	Gly, sarcosine	Ubiquitous	
X_{AG-}	Glu, Asp	Ubiquitous	
Sodium independent			
L	Leu, Ile, Val, Met, Phe, Tyr, Trp, His	Ubiquitous	Yes
T	Trp, Phe, Tyr	Red blood cells, hepatocytes	No
y^+	Arg, Lys, Orn	Ubiquitous	No
asc	Ala, Ser, Cys, Thr	Ubiquitous	Yes

Data from references 10 to 12, with permission.

TABLE 42.8 INTESTINAL EPITHELIAL AMINO ACID TRANSPORT SYSTEMS

TRANSPORT SYSTEM	SOLUTE CARRIER (SLC) CLASSIFICATION	AMINO ACIDS	Na-DEPENDENT
Neutral amino acids			
A	SLC38A2	G, P, A, S, C, Q, N, H, M	Yes
L	SLC3A2, SLC7A8	All neutral AAs except P	
B^0	SLC6A15	P, L, V, I, M	Yes
T	SLC16A10	F, Y, W	Yes
IMINO	SLC6A20	P, hydroxyproline	Yes
ASC	SLC1A5	A, S, C, T, Q	Yes
PAT	SLC36A1	P, G, A, β-alanine, taurine	No, H+
Acidic amino acids			
X^-_{AG}	SLC1A1	E, D	Yes, H+
x−	SLC3A2, SLC7A11	E, cystine	
Basic amino acids			
B^{0+}	SLC6A14	Neutral and basic amino acids, β-alanine	Yes
Y+	SLC7A1	R, K, H, ornithine	
Y^+L	SLC3A2, SLC7A7	K, R, Q, H, M, L	Yes
$b^{0,+}$	SLC3A1, SLC7A9	R, K, ornithine, cystine	No
Dipeptide/tripeptide			
hPept1		Dipeptides and tripeptides	Yes

Amino acids are given in one-letter codes: A, alanine; C, cysteine; D, aspartic acid; E, glutamic acid; F, phenylalanine; G, glycine; H, histidine; I, isoleucine; K, lysine; L, leucine; M, methionine; N, asparagines; P, proline; Q, glutamine; R, arginine; S, serine; T, tyrosine; V, valine; W, tryptophan.

Data from Broer S. Amino acid transport across mammalian intestinal and renal epithelia. Physiol Rev 2008;88:249, with permission.

Almost all protein is absorbed by the time it reaches the distal jejunum, thus only 1% of ingested protein is found in the feces.

Absorbed peptides and amino acids are transported to the liver via the portal vein.

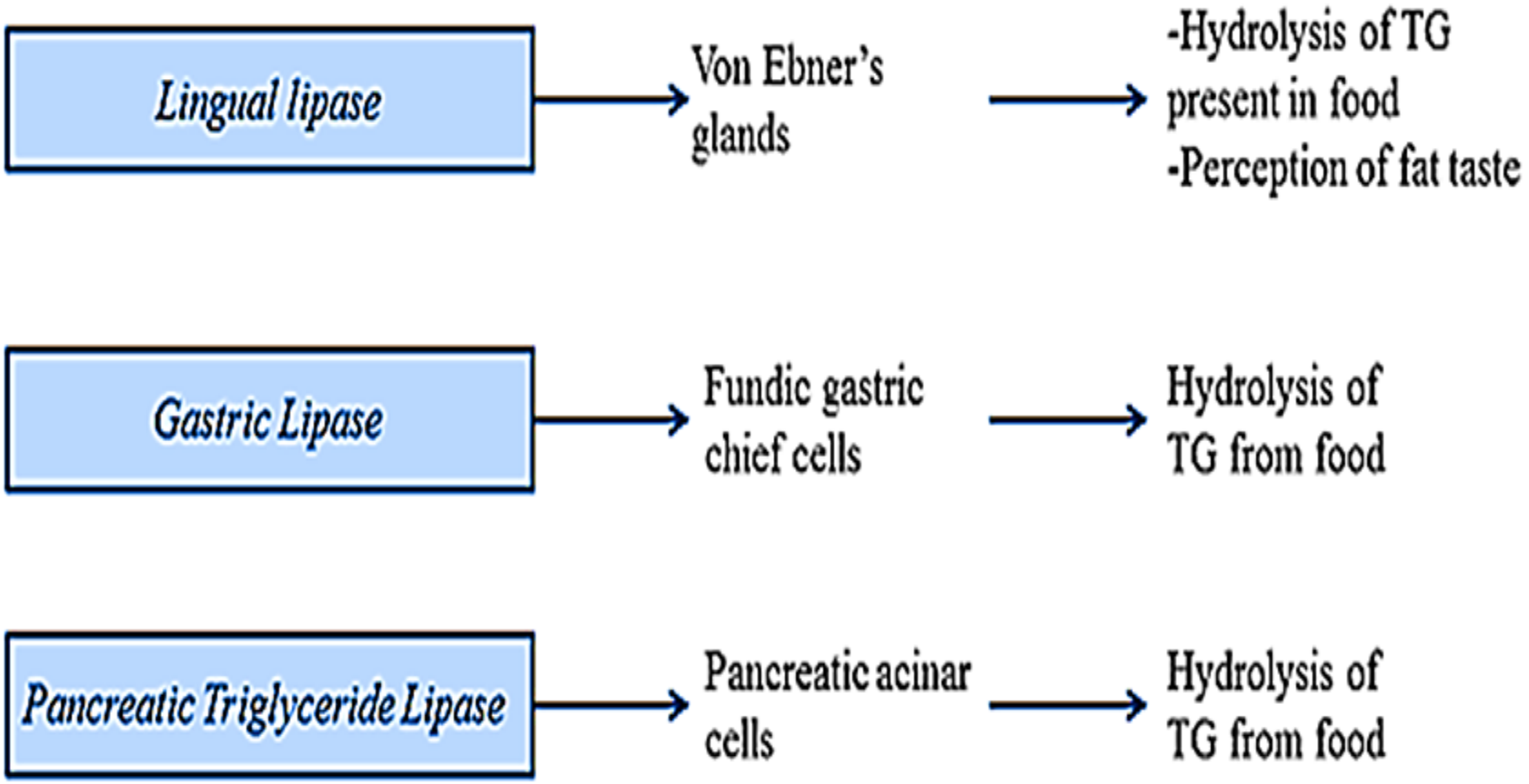
Small amounts of amino acids may remain in the epithelial cells for synthesis of new proteins (e.g. intestinal enzymes).

Lipids

Approximately, 97% of dietary lipids are in the form of triglycerides, and the rest are phospholipids and cholesterol.

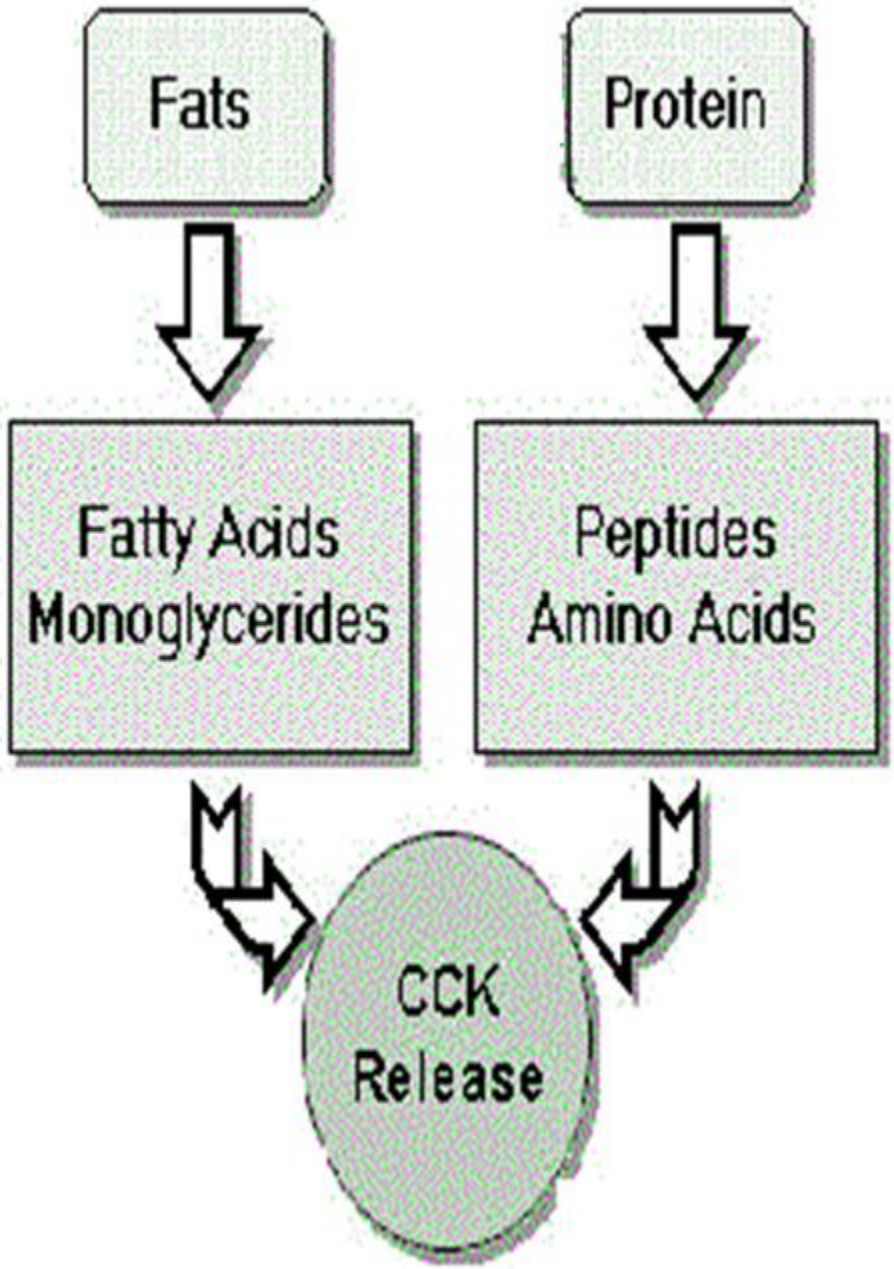
Only small amounts of fat are digested in the mouth with lingual lipase and in the stomach with gastric lipase or tributyrinase, which hydrolyzes short-chain triglycerides (such as those found in butter), into fatty acids and glycerol.

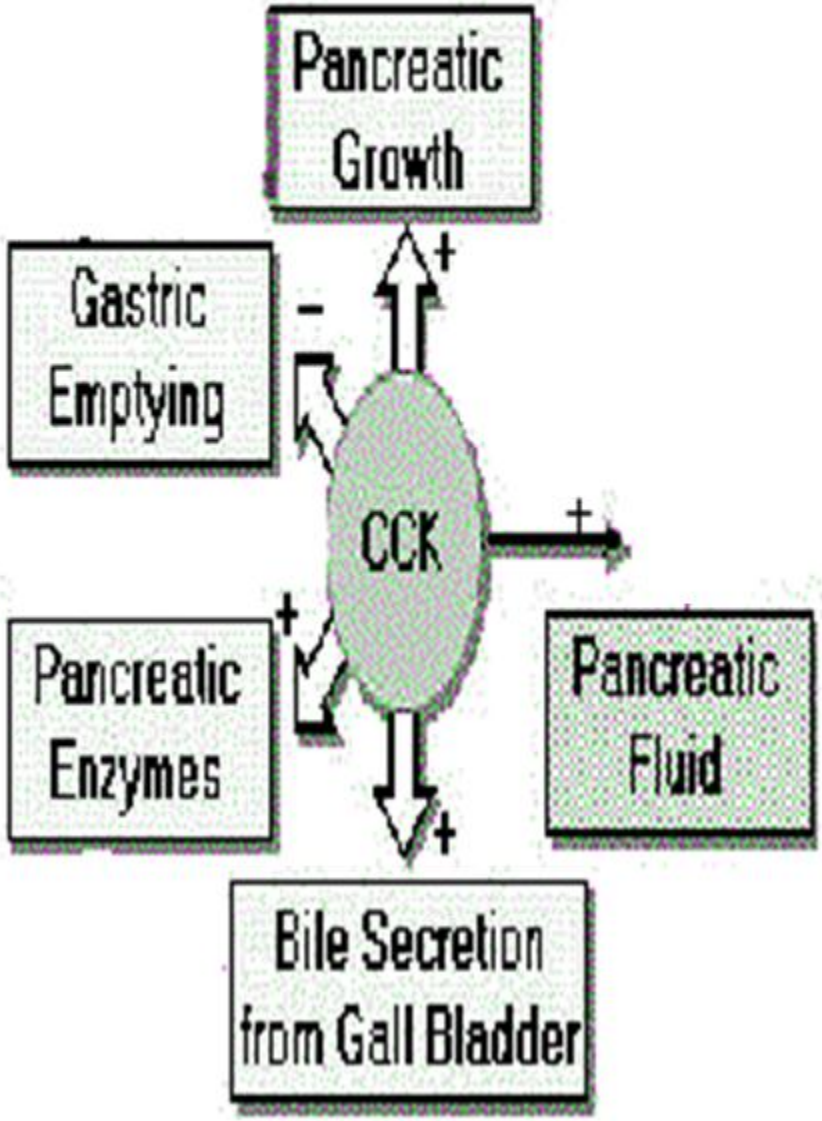
Most fat digestion takes place in the small intestine as a result of the emulsifying action of bile salts and hydrolysis by pancreatic lipase.


Lingual lipase
Von Ebner's glands
-Hydrolysis of TG present in food
-Perception of fat taste
Gastric Lipase
Fundic gastric chief cells
Hydrolysis of TG from food
Pancreatic Triglyceride Lipase
Pancreatic acinar cells
Hydrolysis of TG from food

Entrance of fat and protein into the duodenum stimulates the release of CCK (which stimulates biliary and pancreatic secretions) and enterogastrone, which inhibit gastric secretions and motility, thus slowing the delivery of lipids.

Therefore, a portion of a large, fatty meal may remain in the stomach for 4 hours or longer.


Fats
Protein
Fatty Acids
Monoglycerides
Peptides
Amino Acids
CCK
Release


Pancreatic
Growth
Gastric
Emptying
CCK
Pancreatic
Enzymes
Pancreatic
Fluid
Bile Secretion
from Gall Bladder

The peristaltic action of the small intestine and the emulsification action of bile reduces the fat globules into tiny droplets, thus making them more accessible to digestion by the pancreatic lipase.

The free fatty acids and monoglycerides produced by digestion form complexes with bile salts called micelles, which facilitate passage of the lipids through the watery environment of the intestinal lumen to the brush border.

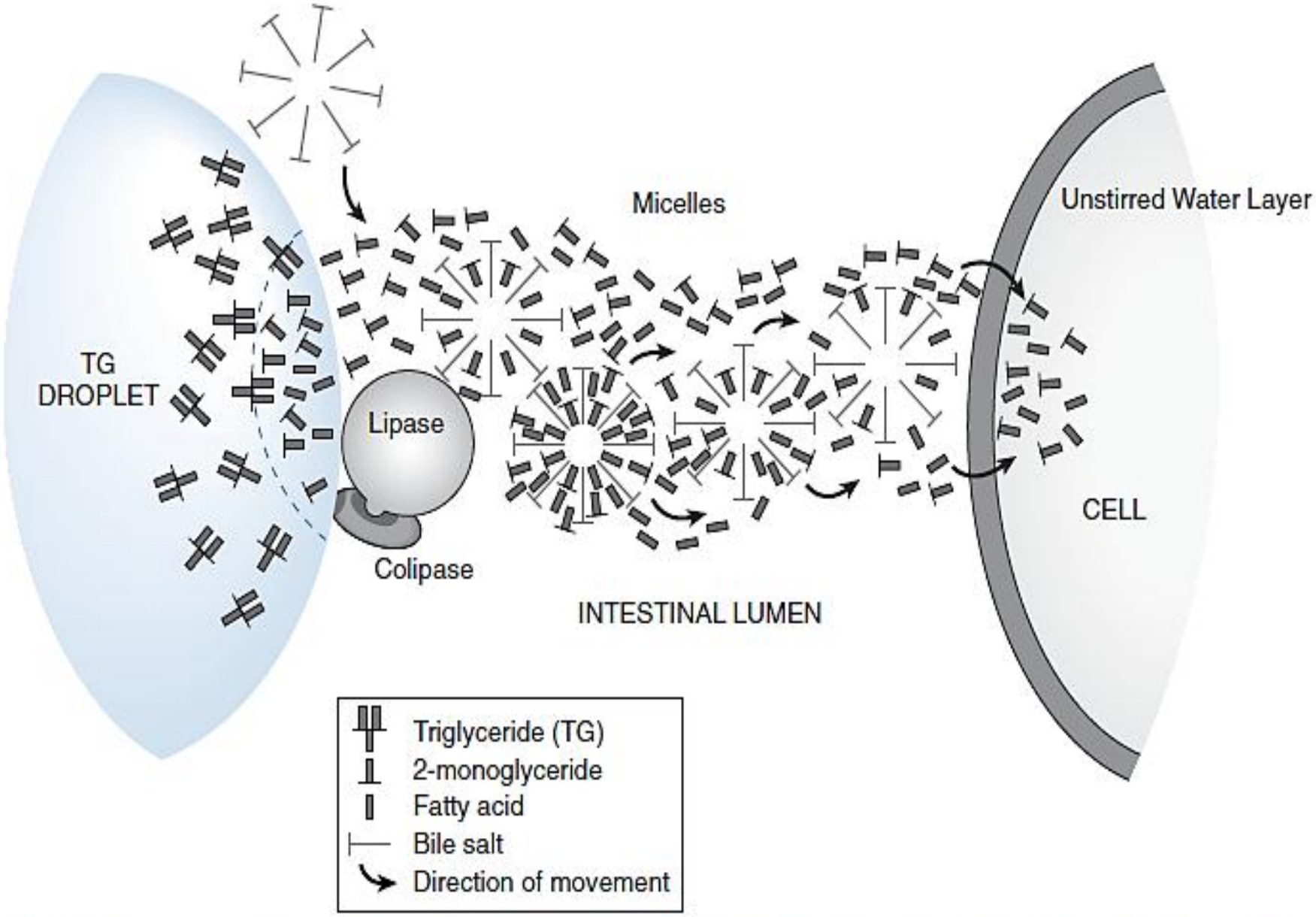
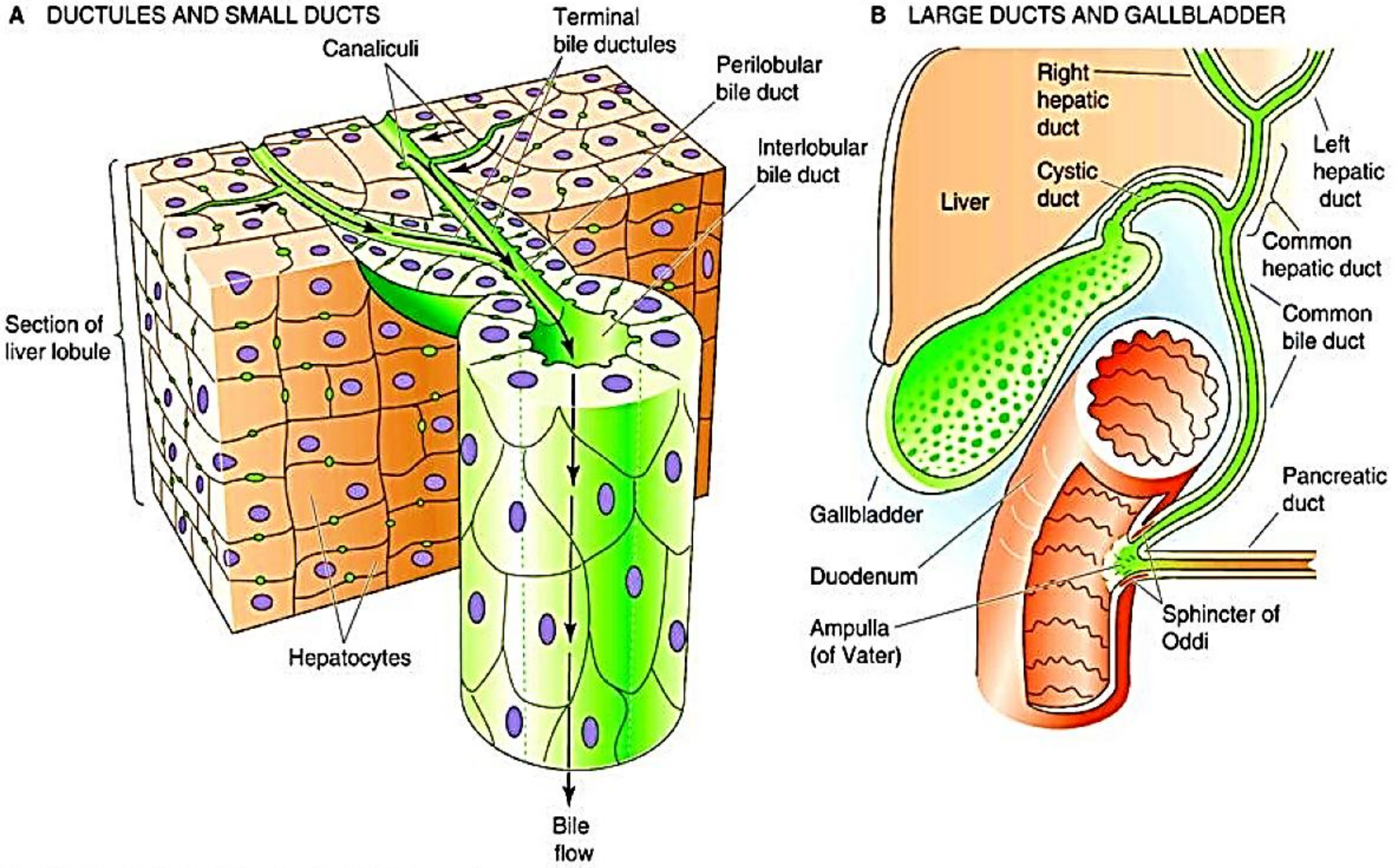


Fig. 4.2. Transport hypothesis of fatty acids and 2-monoglycerides through lipase-mediated hydrolysis, micellar transfer, and cellular uptake stages.

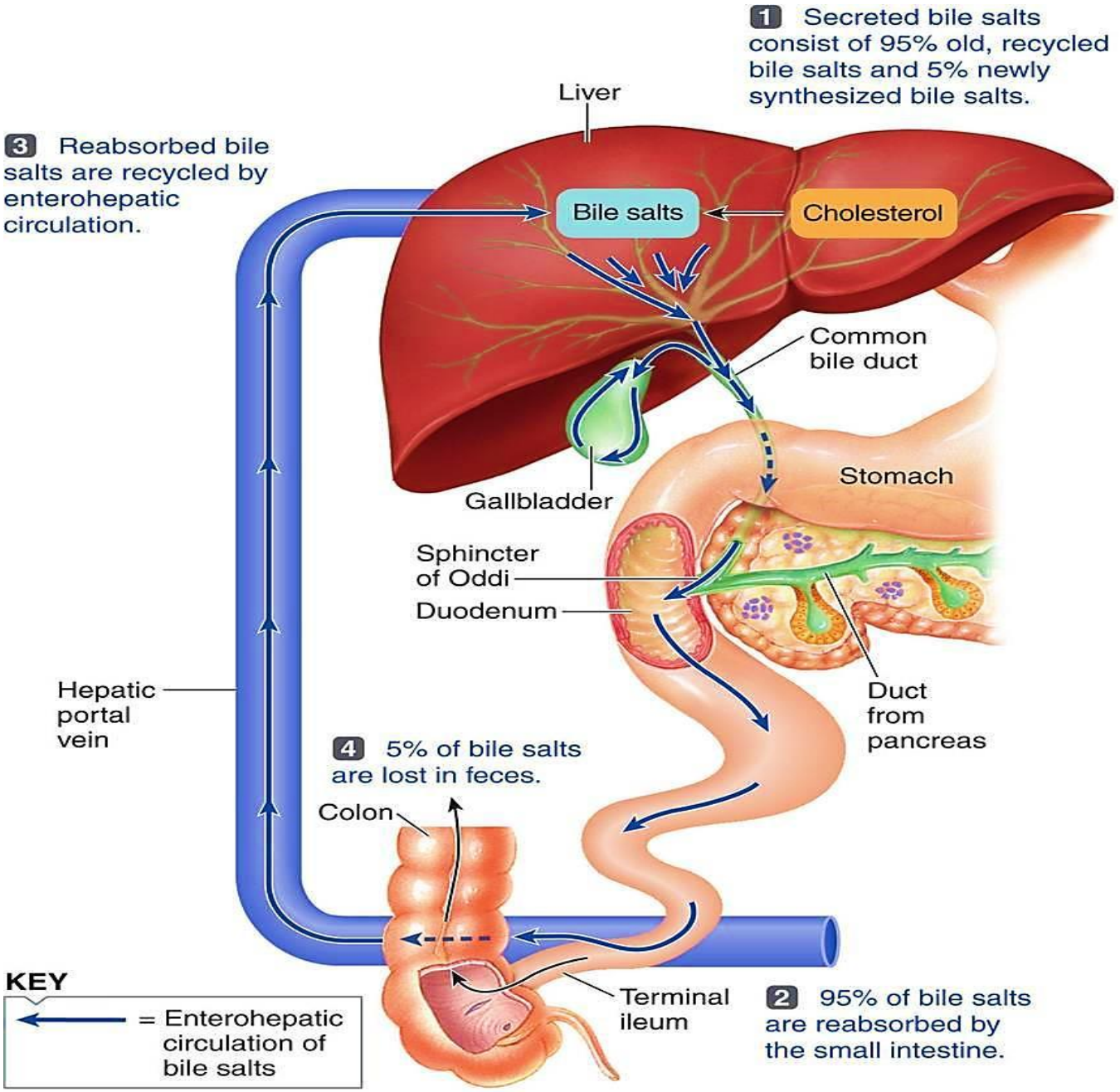
Bile is a liver secretion composed of bile acids (primarily conjugates of cholic and chenodeoxycholic acids with glycine or taurine), bile pigments (which color the feces), inorganic salts, some protein, cholesterol, lecithin, and many compounds such as detoxified drugs.

From its storage organ, the gallbladder, approximately 1 L of bile is secreted daily.

Bile is secreted by the liver, stored in the gall bladder and ejected into the small intestine



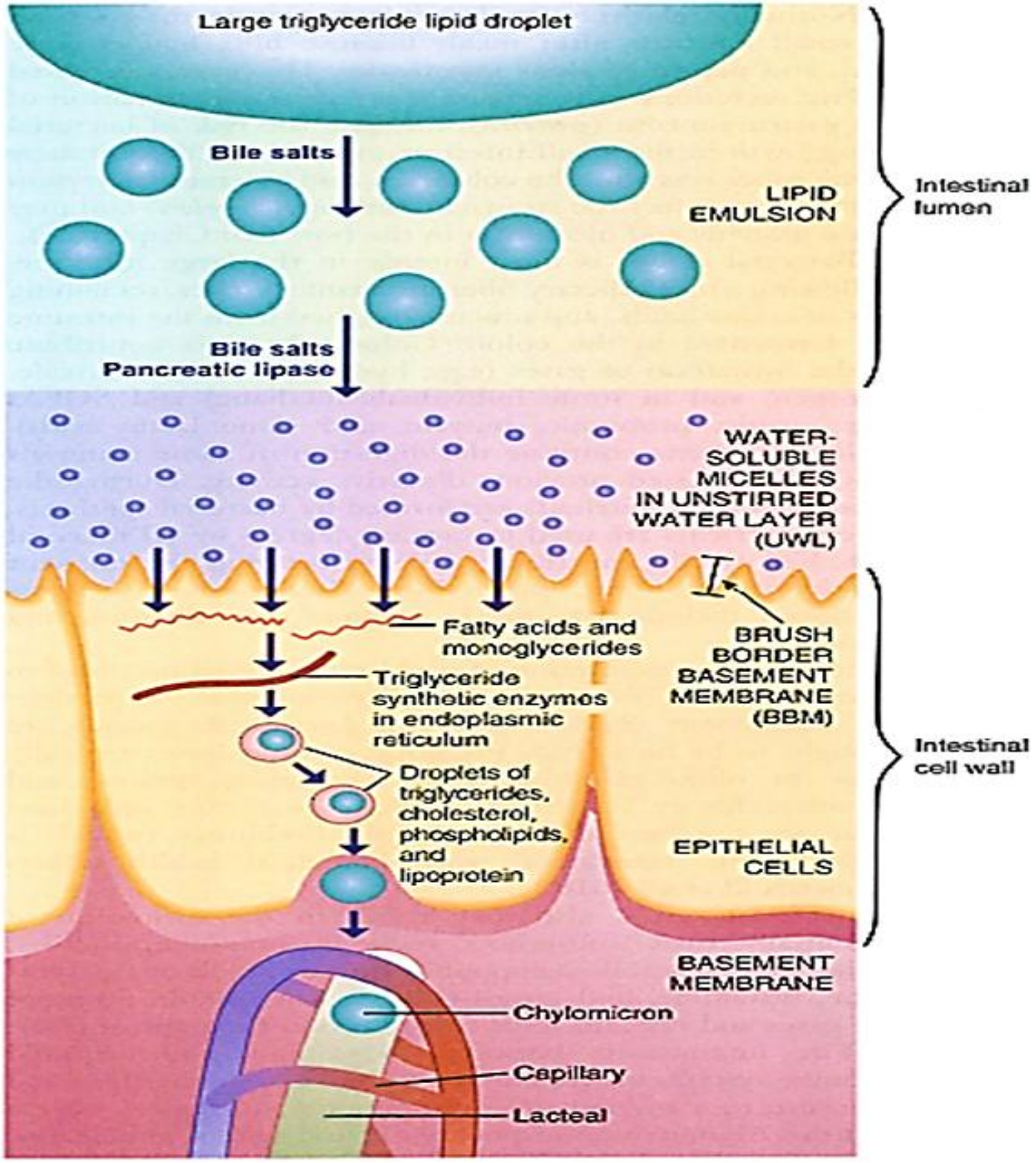
Most of the bile salts are actively reabsorbed in the terminal ileum and returned to the liver to reenter the gut in bile secretions through the process of enterohepatic circulation.


1 Secreted bile salts consist of 95% old, recycled bile salts and 5% newly synthesized bile salts.
Liver
3 Reabsorbed bile salts are recycled by enterohepatic circulation.
Bile salts
Cholesterol
Common bile duct
Gallbladder
Stomach
Sphincter of Oddi
Duodenum
Duct from pancreas
Hepatic portal vein
4 5% of bile salts are lost in feces.
Colon
Terminal ileum
2 95% of bile salts are reabsorbed by the small intestine.
KEY
= Enterohepatic circulation of bile salts

In the mucosal cells the fatty acids and monoglycerides are reassembled into new triglycerides.

These triglycerides, along with cholesterol, fat-soluble vitamins, and phospholipids, are surrounded by a lipoprotein coat, forming chylomicrons.

Chylomicrons pass into the lymphatic system and are transported to the thoracic duct and emptied into the systemic circulation at the junction of the left internal jugular and left subclavian veins.


Large triglyceride lipid droplet
Bile salts
LIPID EMULSION
Intestinal lumen
Bile salts
Pancreatic lipase
WATER-SOLUBLE MICELLES IN UNSTIRRED WATER LAYER (UWL)
Fatty acids and monoglycerides
BRUSH BORDER BASEMENT MEMBRANE (BBM)
Triglyceride synthetic enzymes in endoplasmic reticulum
Droplets of triglycerides, cholesterol, phospholipids, and lipoprotein
Intestinal cell wall
EPITHELIAL CELLS
BASEMENT MEMBRANE
Chylomicron
Capillary
Lacteal

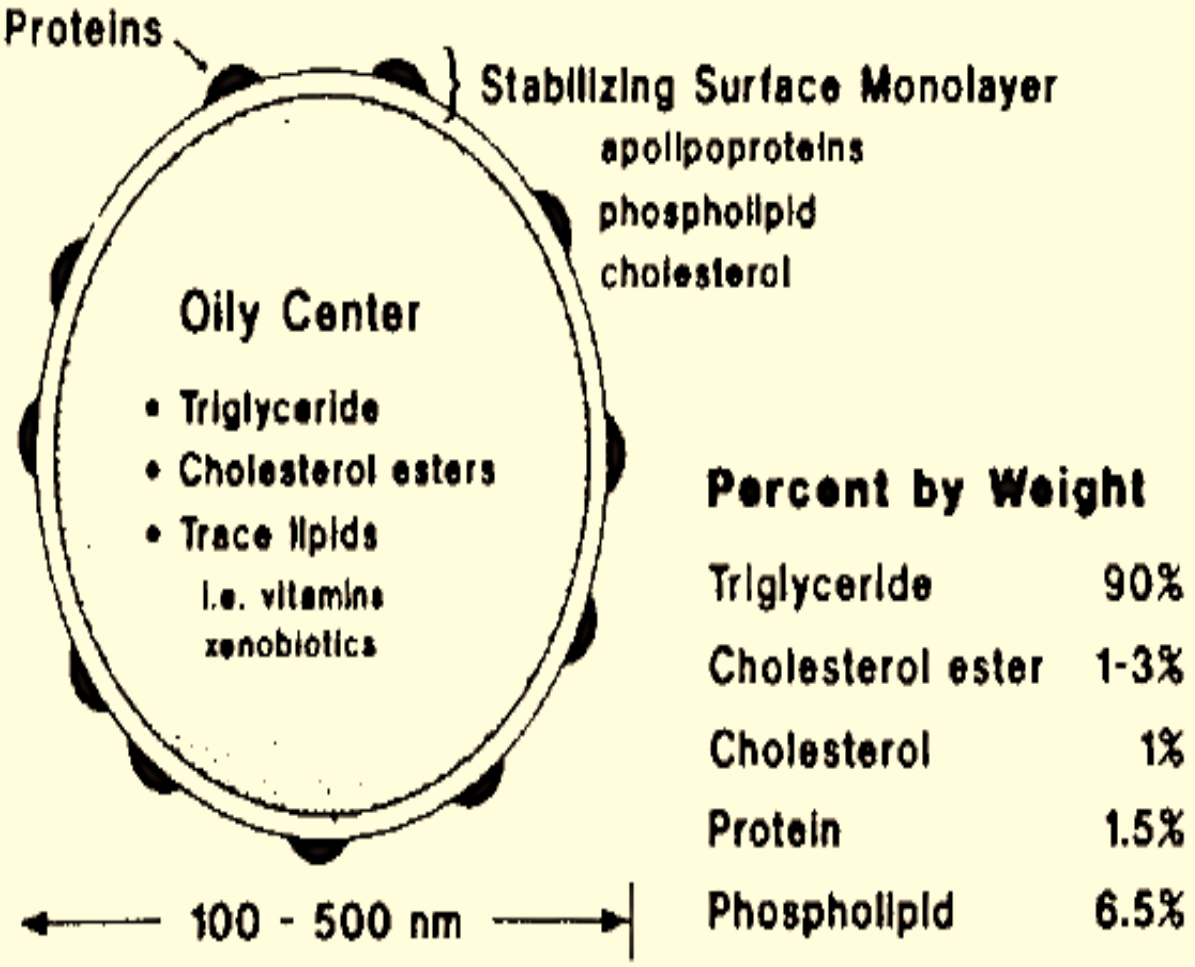
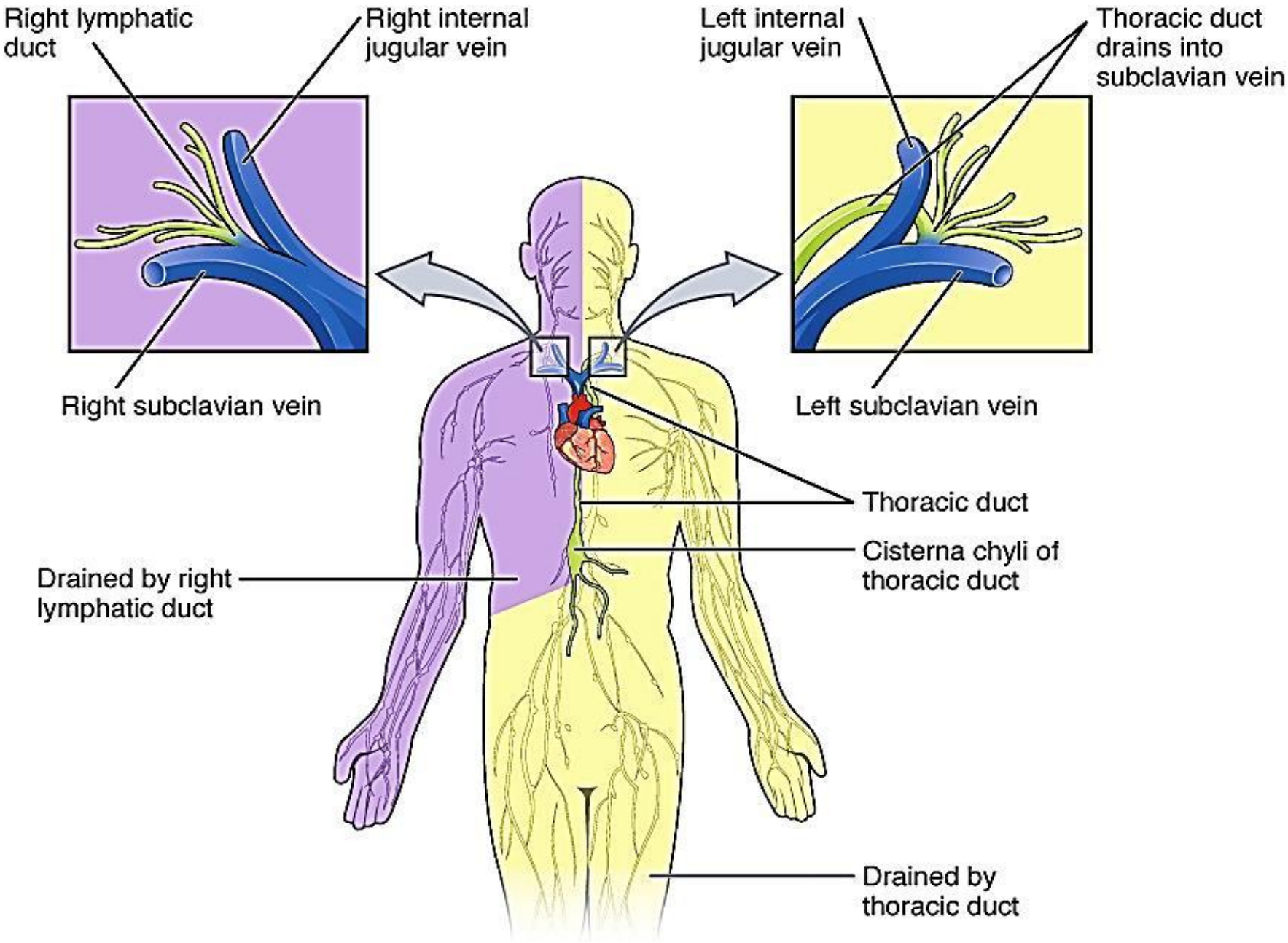
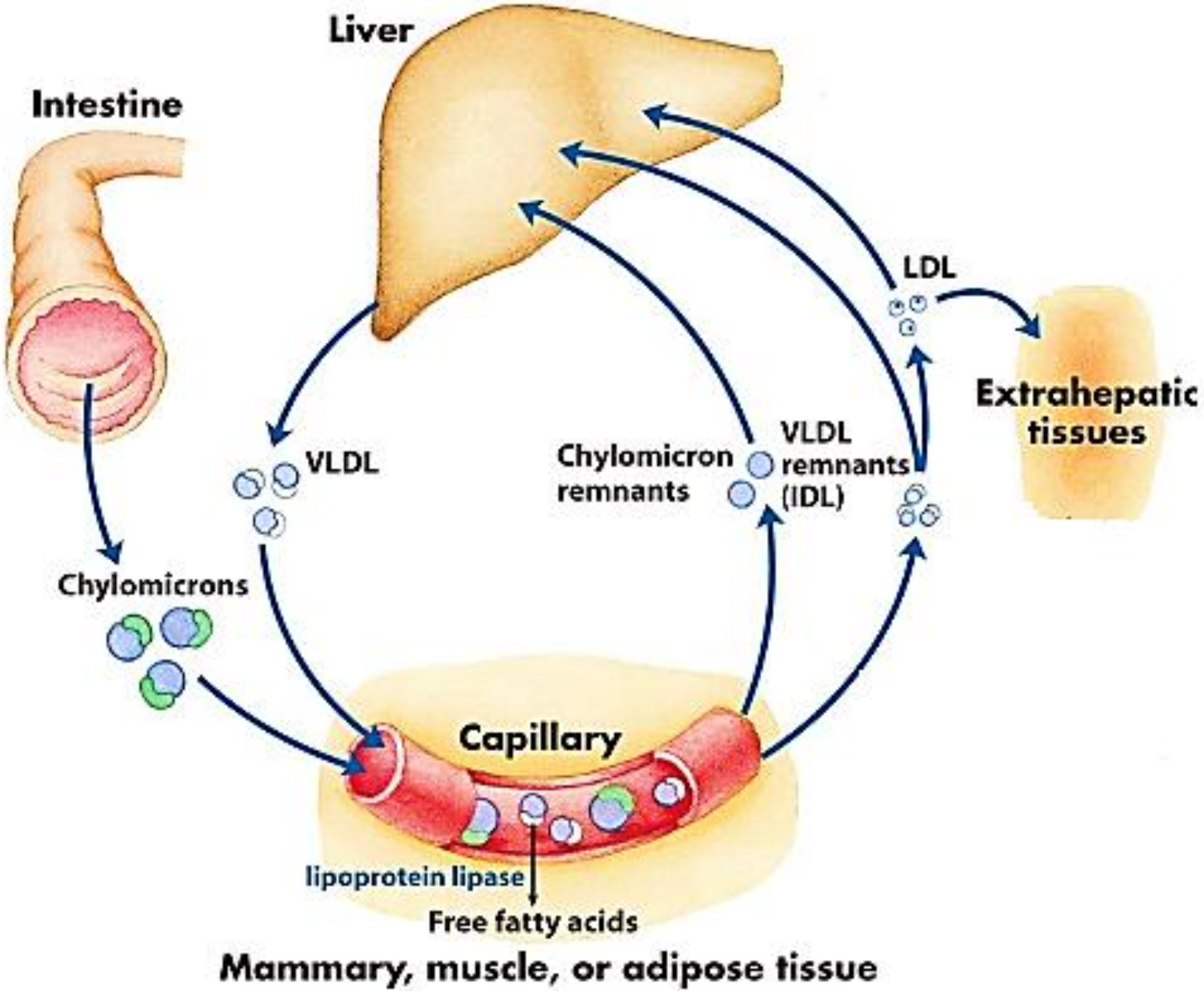


Fig. 42.13. Chylomicrons are fat droplets that are coated with a monolayer of phospholipid and cholesterol. Dispersed in the monolayer are apoproteins (Apo) A-1, apoA-IV, and Apo B and probably also some Apo C-11 and Apo C-111. These proteins help direct the tissue uptake and catabolism of the chylomicrons. In the circulation, chylomicrons also acquire additional apoproteins. Although triglyceride is the major lipid carried in chylomicrons, they are also carriers of cholesterol, fat-soluble vitamins, and small amounts of many other trace lipophilic molecules. (Reprinted with permission from Patton JS, Hoffman AF. Lipid Digestion. Undergraduate Teaching Project, Unit 19. Bethesda, MD: American Gastroenterological Association, 1986.)


Right lymphatic duct
Right internal jugular vein
Left internal jugular vein
Thoracic duct drains into subclavian vein
Right subclavian vein
Left subclavian vein
Thoracic duct
Cisterna chyli of thoracic duct
Drained by right lymphatic duct
Drained by thoracic duct

The chylomicrons are then carried through the bloodstream to several tissues, including liver, adipose tissue, and muscle.

In the liver, triglycerides from the chylomicrons are repackaged into very low-density lipoproteins and transported primarily to the adipose tissue for metabolism and storage.


Liver
Intestine
LDL
Extrahepatic tissues
VLDL
Chylomicron remnants
VLDL remnants (IDL)
Chylomicrons
Capillary
lipoprotein lipase
Free fatty acids
Mammary, muscle, or adipose tissue

The fat-soluble vitamins A, D, E, and K are also absorbed in a micellar fashion, although water-soluble forms of vitamins A, E, and K supplements and carotene can be absorbed in the absence of bile acids.

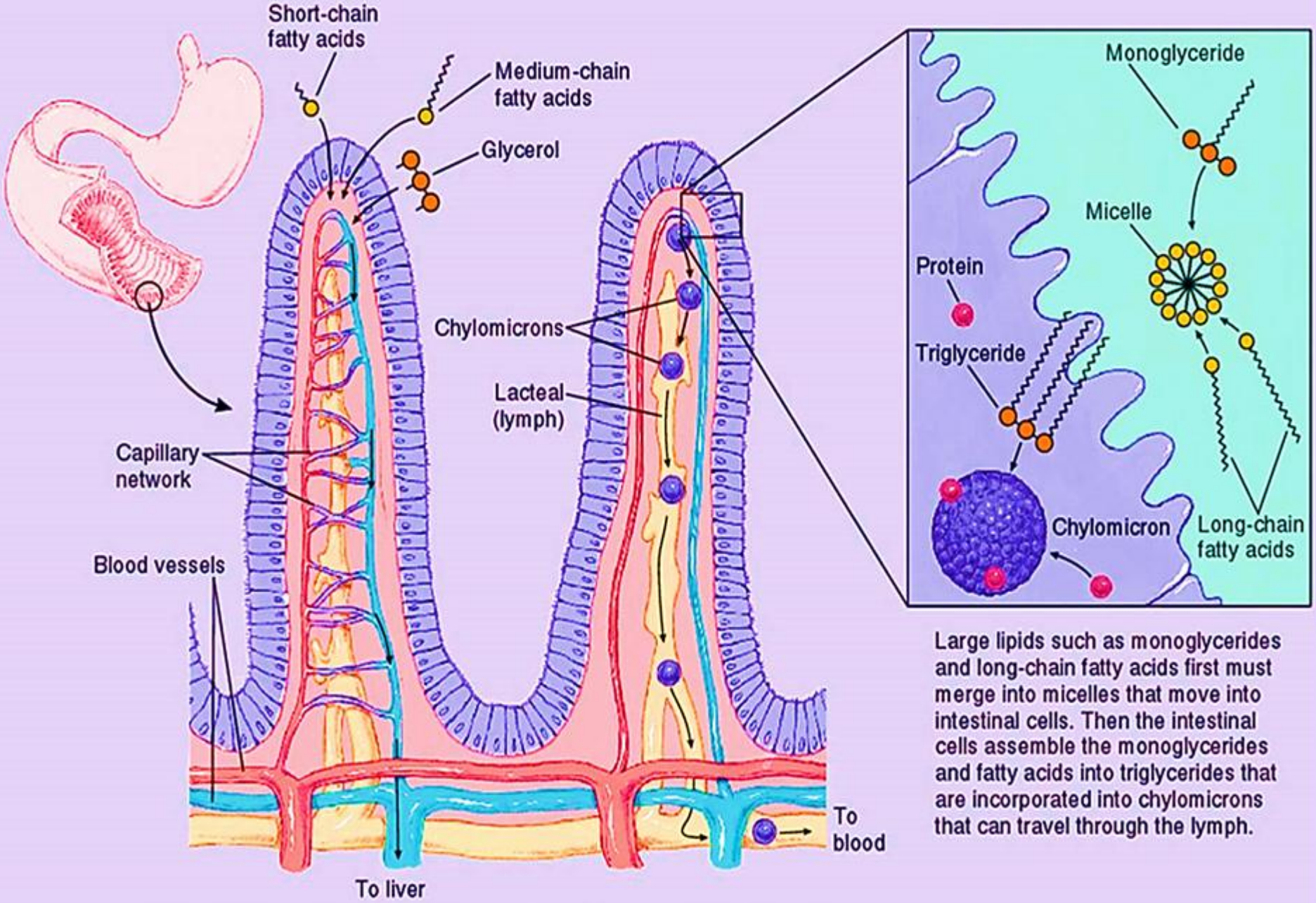
Normally, 95% to 97% of ingested fat is absorbed into lymph vessels.

Increased motility, intestinal mucosal changes, pancreatic insufficiency, or the absence of bile can decrease fat absorption.

When undigested fat appears in the feces, the condition is known as steatorrhea.

Because of their shorter length and thus increased solubility, fatty acids of 8 to 12 carbons (i.e. medium-chain fatty acids) can be absorbed directly into mucosal cells without the presence of bile and micelle formation, where they are able to go directly without esterification into the portal vein.

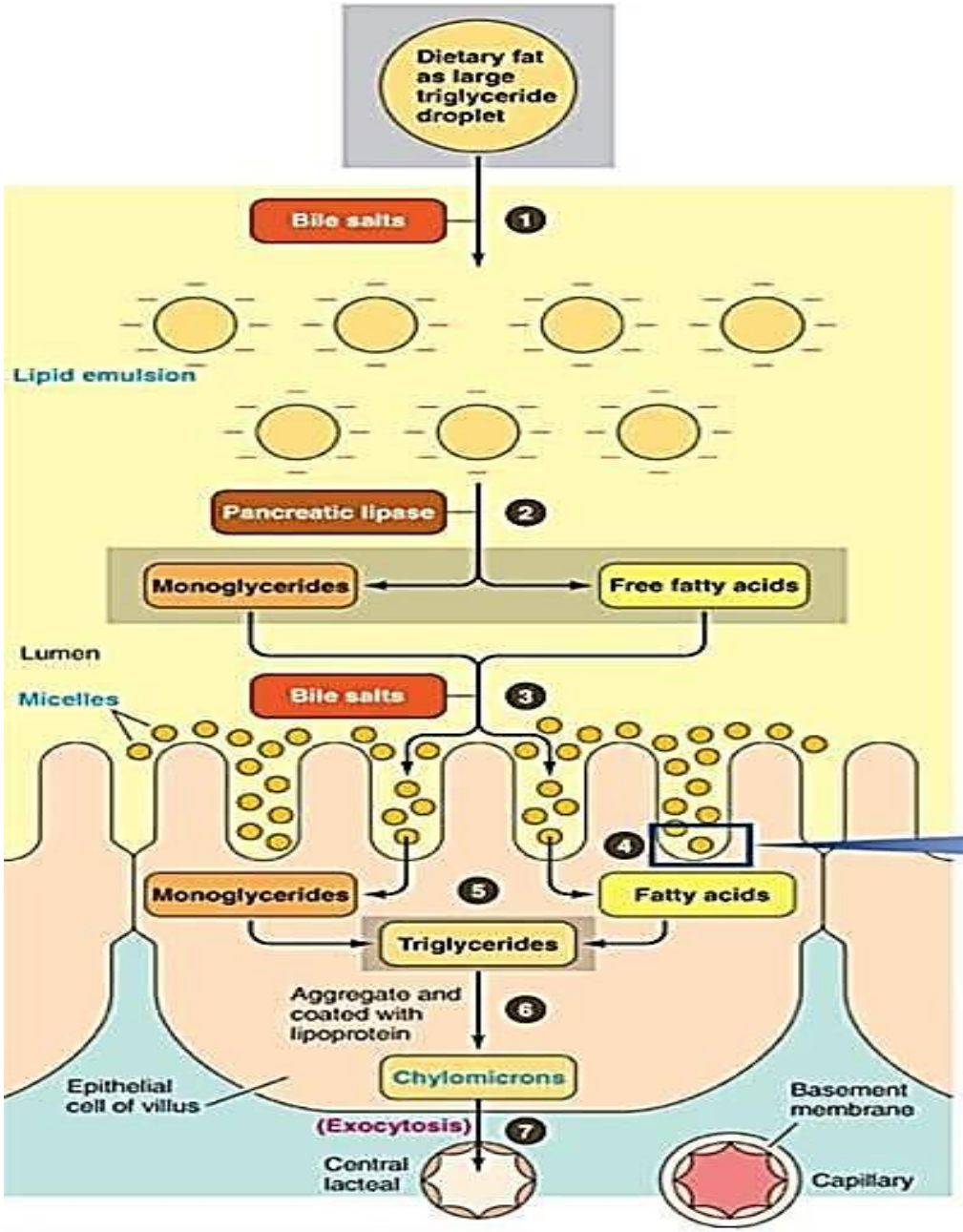
Due to these characteristics, medium-chain triglycerides (MCTs), which have medium-chain fatty acids, are clinically valuable for individuals who lack necessary bile salts for long-chain fatty acid metabolism and transport.



Large lipids such as monoglycerides and long-chain fatty acids first must merge into micelles that move into intestinal cells. Then the intestinal cells assemble the monoglycerides and fatty acids into triglycerides that are incorporated into chylomicrons that can travel through the lymph.

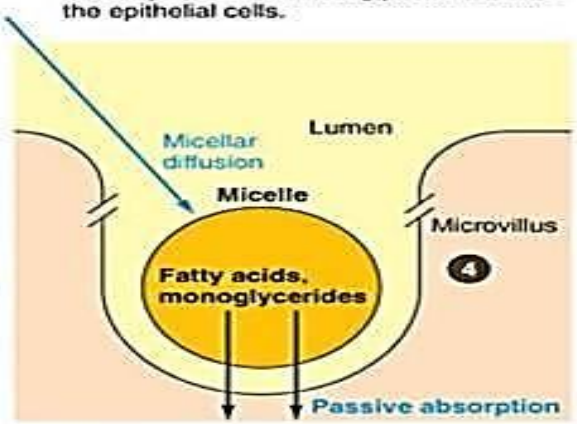
The end products of fat digestion are mostly monoglycerides, some fatty acids, and very little glycerol. Glycerol and short- and medium-chain fatty acids can move directly into the bloodstream.

Summary of fat digestion and absorption



Because fat is not soluble in water, it must undergo a series of transformations in order to be digested and absorbed.

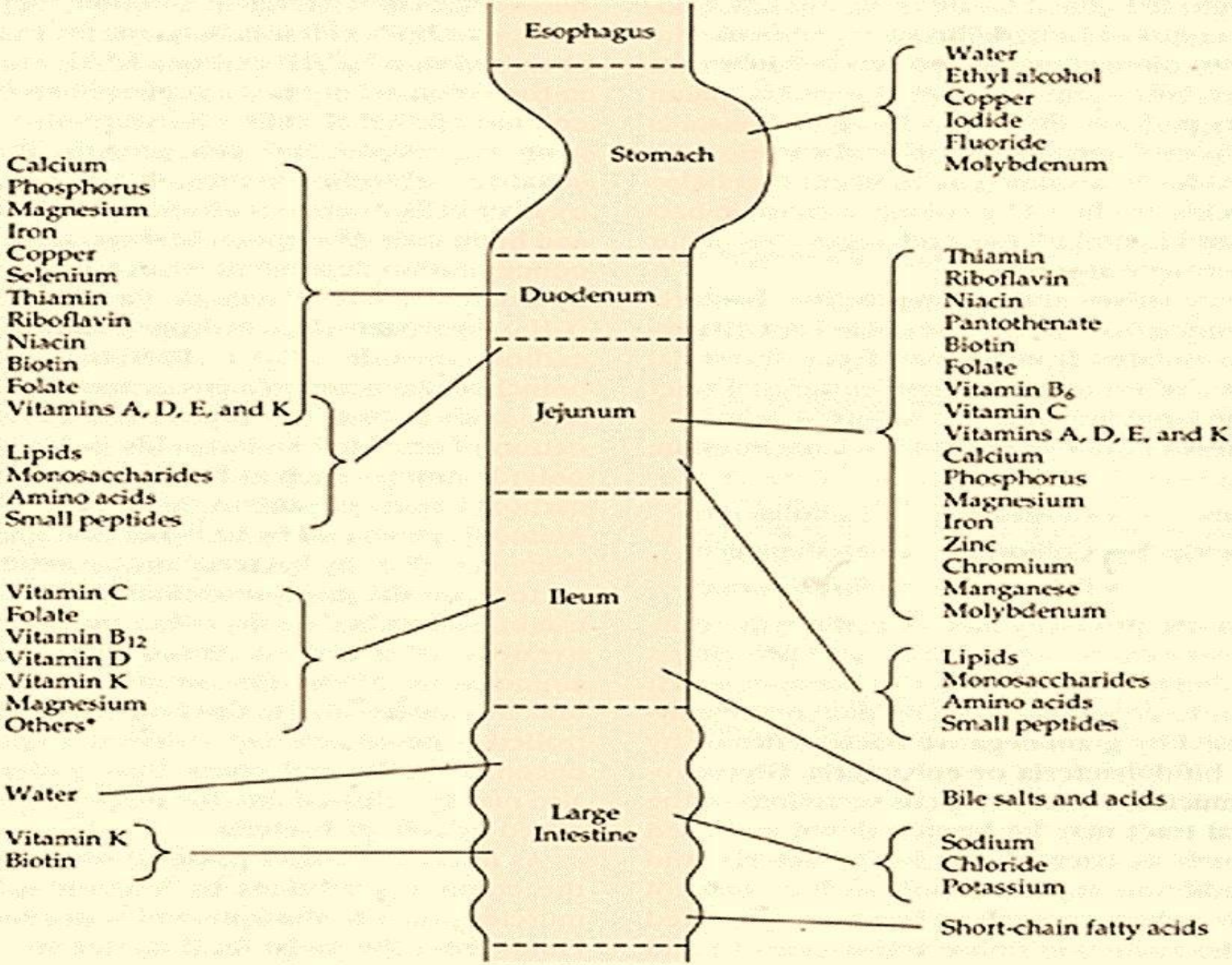
1. Dietary fat in the form of large fat globules composed of triglycerides is emulsified by the detergent action of bile salts into a suspension of smaller fat droplets. This lipid emulsion prevents the fat droplets from coalescing and thereby increases the surface area available for attack by pancreatic lipase.
2. Lipase hydrolyzes triglycerides into monoglycerides and free fatty acids.
3. These water-insoluble products are carried in the interior of water-soluble micelles, which are formed by bile salts and other bile constituents, to the luminal surface of the small intestine epithlial cells.
4. When a micelle approaches the absorptive epithelial surface, the monoglycerides and fatty acids leave the micelle and passively diffuse through the lipid bilayer of the luminal membranes.
5. The monoglycerides and free fatty acids are resynthesized into triglycerides inside the epithelial cells.



6. These triglycerides aggregate and are coated with a layer of lipoprotein to form water-soluble chylomicrons, which are extruded through the basal membrane of the cells by exocytosis.
7. Chylomicrons are unable to cross the basement membrane of blood capillaries, so instead they enter the lympathic vessels, the central lacteals.

Vitamins and Minerals

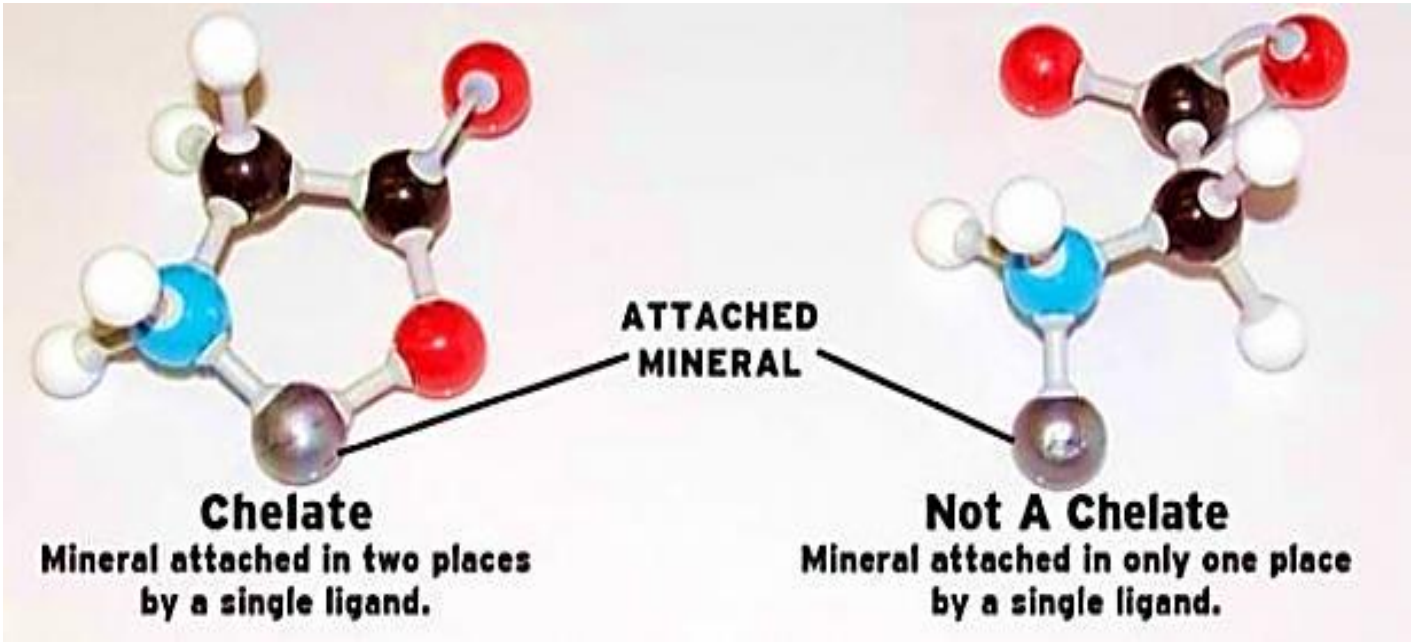
Vitamins and minerals from foods are made available as macronutrients and are digested and absorbed primarily in the small intestine.

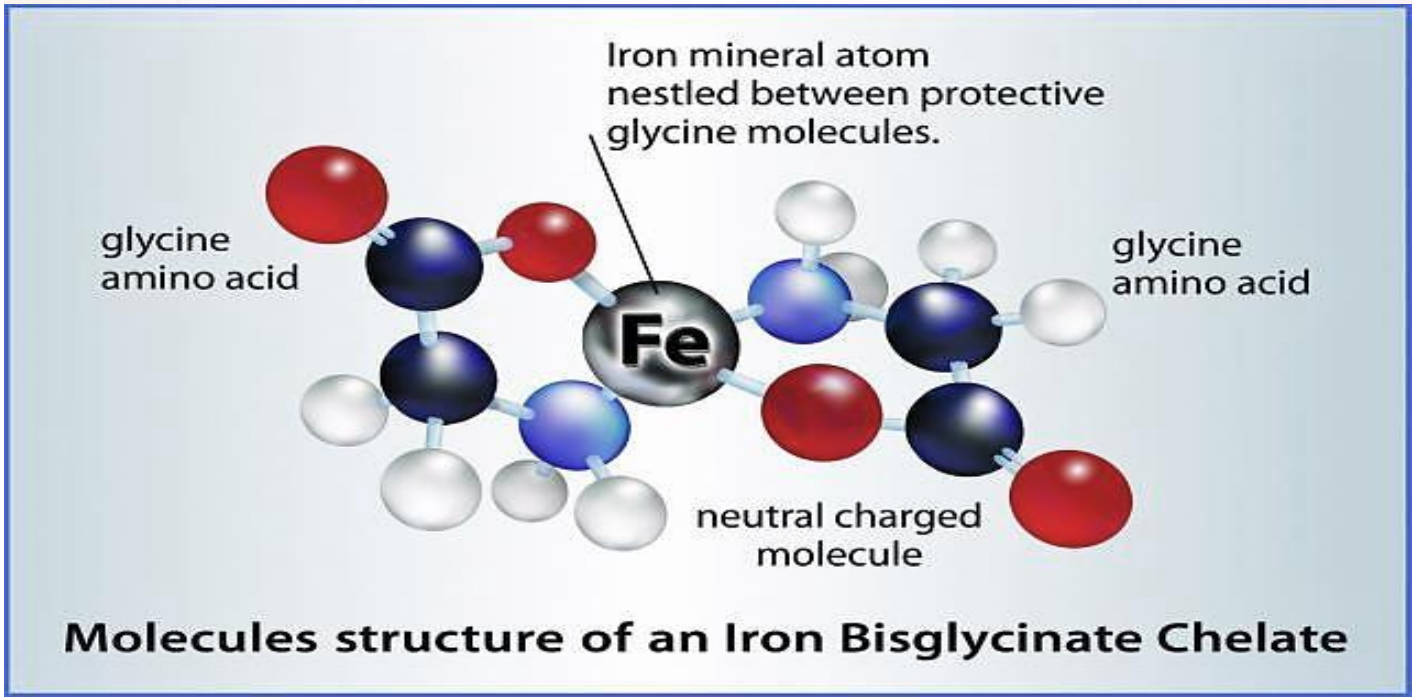

Esophagus
Stomach
Duodenum
Jejunum
Ileum
Large Intestine
Water
Ethyl alcohol
Copper
Iodide
Fluoride
Molybdenum
Calcium
Phosphorus
Magnesium
Iron
Copper
Selenium
Thiamin
Riboflavin
Niacin
Biotin
Folate
Vitamins A, D, E, and K
Lipids
Monosaccharides
Amino acids
Small peptides
Thiamin
Riboflavin
Niacin
Pantothenate
Biotin
Folate
Vitamin B6
Vitamin C
Vitamins A, D, E, and K
Calcium
Phosphorus
Magnesium
Iron
Zinc
Chromium
Manganese
Molybdenum
Vitamin C
Folate
Vitamin B12
Vitamin D
Vitamin K
Magnesium
Others*
Lipids
Monosaccharides
Amino acids
Small peptides
Water
Bile salts and acids
Vitamin K
Biotin
Sodium
Chloride
Potassium
Short-chain fatty acids

At least some vitamins pass unchanged from the small intestine into the blood by passive diffusion, but several different mechanisms might be used to transport individual vitamins across the GI mucosa.

Mineral absorption is more complex, especially the absorption of the cation minerals.

These cations, are made available for absorption by the process of chelation, in which a mineral is bound to a ligand, usually an acid, an organic acid, or an amino acid, so that it is in a form absorbable by intestinal cells.





Molecules structure of an Iron Bisglycinate Chelate

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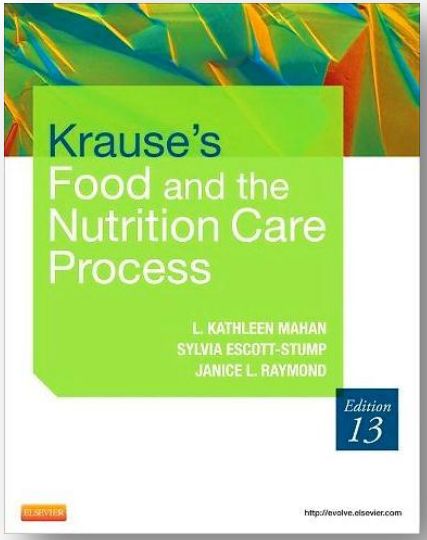
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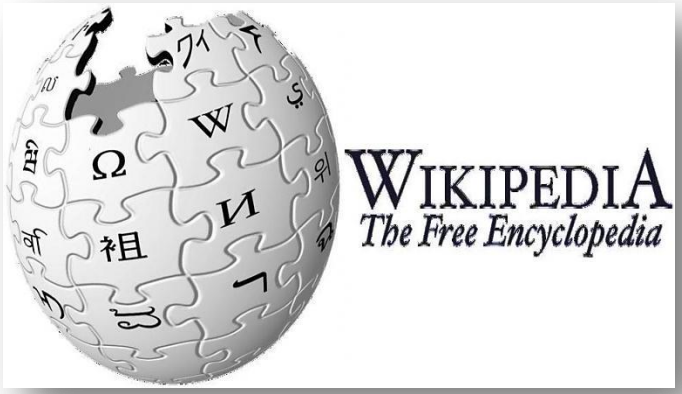
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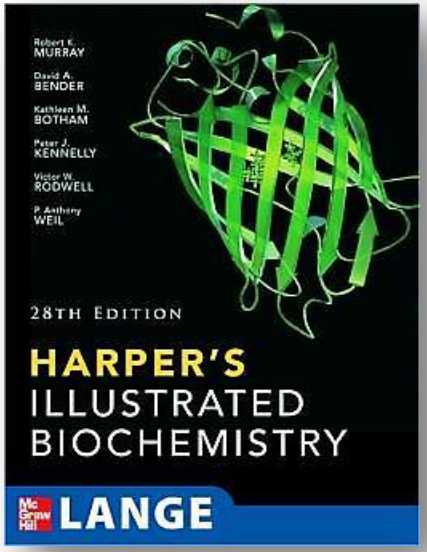
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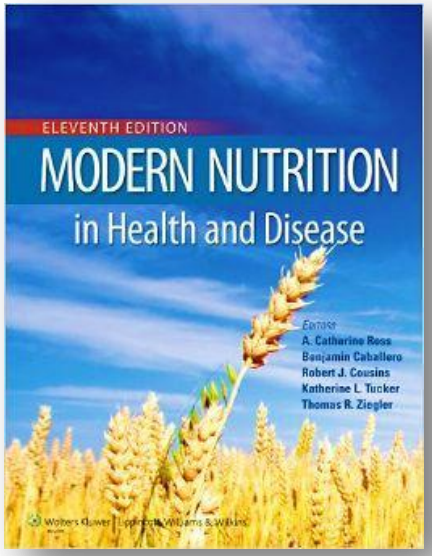
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