UNIT 5 DIGESTION, ABSORPTION AND TRANSPORT OF CARBOHYDRATES, PROTEINS AND LIPIDS

Structure

5.1 INTRODUCTION

Nutrition emphasizes the role of foodstuffs in meeting the energy and specific requirements of the body for continuation of cellular activity. Although food assumes a wide variety of forms, it is categorized into major six chemical forms i.e. carbohydrates, proteins, lipids, vitamins, minerals and water and these are collectively termed as 'nutrients'. The first three units in this block focused on the chemistry of these nutrients and their properties. In this unit, we shall deal with their digestion, absorption and transportation.

Next, once ingested, what happens to these nutrients in our body? These nutrients, as you may already know, are utilized to perform the various functions i.e. provide energy, body building, protection against diseases etc. in our body. Of the major six nutrients, only carbohydrates, proteins and lipids can give energy. The ingested food material is broken down into smaller constituents which are then passed into the gastrointestinal tract and then into the bloodstream. The process through which the major nutrients namely carbohydrates, proteins and lipids are converted to simple substances and then passed into the gastrointestinal tract and then into the bloodstream is called *digestion* and *absorption*. In this unit we shall focus on the processes of digestion, absorption and transport of nutrients in our body, with emphasis on the role of various enzymes which facilitate the process.

Objectives

After studying this unit, you will be able to:

- recognize the organs of the digestive system and their functions,
- understand the process of digestion in stomach and intestine,
- discuss the role of various enzymes in facilitating the digestion process,
- explain the hormonal and neural control of secretions of salivary glands, gastric glands, pancreas, liver and intestine, and

- differentiate between the types of absorption and transport of final end products across the intestinal brush border into the portal and lymphatic system.

5.2 DIGESTION, ABSORPTION AND TRANSPORT - BASIC CONCEPT

What is digestion? The ingested food material is broken down into smaller constituents which are assimilable by the blood. *The process through which the major nutrients namely carbohydrates, proteins and lipids are converted to simple sugars, amino acids, fatty acids and glycerol respectively, while passing from mouth to small intestine, constitutes digestion.* The process of digestion is facilitated with the help of secretions from salivary glands, stomach, pancreas and liver. Both hormonal and neural controls regulate these secretions. Microvilli of the small intestine are the major site of absorption. So then what is absorption? *Absorption involves the transfer of materials through the mucosa of the alimentary tract into blood and lymph vessels.* The transfer comprises of different transport mechanisms. In the next few sections we shall learn about each of these processes i.e. digestion, absorption and transport of carbohydrates, proteins and lipids. We shall begin with digestion.

5.3 DIGESTION

Digestive enzymes break down food particles into smaller units. You will see that the final breakdown products of protein digestion are single *amino acids* or *small chains of two or three amino acids.* The final products of carbohydrate digestion are *monosaccharides.* The final digestive products of triacylglycerol digestion are *free fatty acids* and *glycerol* and *monoacylglycerols.* Vitamins, minerals, water and some larger fat-like compounds such as cholesterol are not broken down before they are absorbed.

Where does the digestion of food occur in our body? Obviously, it occurs in the digestive system. You may recall reading about the anatomy of the digestive system in the Applied Physiology Course, Unit 6. If you have not gone through this Unit, we suggest you read the Unit now, as it will help in understanding the concepts explained in this Unit. The human digestive system is a coiled, muscular tube (6-9 meters long when fully extended) extending from the mouth to the anus. Several specialized compartments occur along this length- mouth, pharynx, orsophagus, stomach, small intestine, large intestine and anus. Basically, the digestive system is made up of two groups of organs:

- *Alimentary tract,* which includes mouth, pharynx, oesophagus, stomach, small intestine, large intestine, appendix, rectum, anal canal, and
- *Accessory organs,* which include tongue, teeth, salivary glands, liver, gall bladder and pancreas.

The major function of the digestive system is to ingest the food materials, digest it to absorbable end products, absorb these products and eliminate the unusable material. That sounds simple. But actually the process involved is not all that simple. Starting from the mouth, the process of digestion through the different compartments of the digestive system is discussed next.

5.3.1 Digestion in the Mouth

The mouth receives food. The tongue serves in swallowing, manipulating the food for chewing and in perceiving taste. The teeth mechanically subdivide the food for easier digestion. Then, there are the salivary glands. There are three pairs of salivary glands namely parotid, submaxillary and sublingual which secrete the colourless viscous fluid called *'saliva'.* Saliva helps in swallowing the food by lubricating the food and the neutral pH of saliva prevents the decalcification of teeth and keeps the mouth clean. In the mouth, is also present the salivary amaylase, originally called *ptyalin.* The presence of *salivary amylase* starts the starch digestion by breaking it into *dextrins.* Dextrins are *polysaccharides containing fewer simple sugar units than starches.* The salivary secretion is controlled by nervous reflexes. From the mouth, the partly digested food enters the stomach. What happens there? Let's find out.

5.3.2 Digestion in the Stomach

To understand the digestion mechanism in the stomach, it is important to know about the anatomy of the stomach. Look up Unit 6, in the Applied Physiology Course. You would notice that the stomach is a 'J' shaped organ and secretes gastric juice. The major components of gastric juice are hydrochloric acid and the enzyme *pepsin,* which is secreted in an inactive form called *pepsinogen.* Small amount of lipase is also produced but remains inactive because of the acidic nature of gastric juice. *Rennin* is present only in infants and helps in the digestion of milk protein *'casein'.* Hydrochloric acid (pH 1.2 – 1.5) activates the inactive pepsinogen to the active form 'pepsin' as indicated in the Figure 5.1. Hydrochloric acid denatures the food proteins for easy digestion. The germicidal effect of hydrochloric acid also prevents the growth of microorganisms in the stomach.

Digestion of proteins is initiated in the stomach by pepsin. Pepsin acts upon food proteins and converts them to proteoses and peptones which are large polypeptide derivatives as can be seen in Figure 5.1. Pepsin is an endopeptidase since it hydrolyses peptide bonds within the main polypeptide structure. Pepsin specifically acts upon the peptide bonds formed by amino acids with an aromatic ring (e.g. tyrosine) or dicarboxylic amino acid i.e. amino acids with 2 COOH groups (e.g. glutamate). You may recall reading about the structure of amino acid earlier in Unit 2 under the protein section.

In infants, the presence of rennin helps in digestion of casein to paracasein which is then acted upon by pepsin.

$$\text{Pepsinogen} \xrightarrow{\text{HCl}} \text{Pepsin + Peptides}$$

The pepsin formed as an active proteolytic enzyme activates the remainder of the pepsinogen molecules by proteolytically converting them to pepsin.

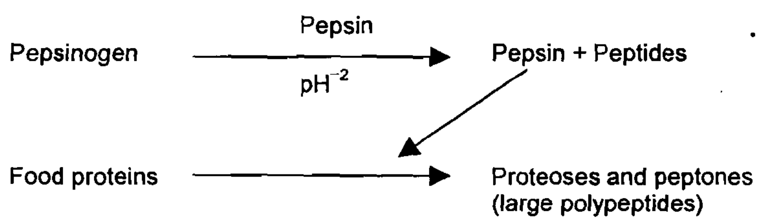

Figure 5.1: Role of pepsin

A word about the control of gastric secretion. Gastric secretion is initiated by nervous reflexes and the continued secretion is controlled by the hormone 'gastrin' produced by the stomach. Histamine, the decarboxylated amino acid 'histidine' also stimulates gastric juice production.

Next, from the stomach the partly digested food passes into the intestine via the pancreas. We shall look at the role of pancreas in digestion now.

5.3.3 Role of Pancreas in Digestion

Pancreatic juices secreted from the pancreas aid in digestion of the food. About 600-800 ml of fluid i.e. the pancreatic juice is secreted per day by pancreas. Pancreatic juice is alkaline in nature (pH about 8.0) and contains both organic and inorganic substances. The enzyme components are *trypsin, chymotrypsin, elastase* and *carboxypeptidase*, all of which are secreted as inactive precursors called *zymogens*. The other enzymes are *amylase, lipase, cholesteryl ester hydrolase, phospholipase, ribonucleases, deoxyribonucleases* and *phosphodiesterases.* Sodium, chloride and bicarbonate are the major inorganic constituents. Before we proceed further, let us understand what we mean by zymogens. Zymogen is *actually the enzyme molecule synthesized, but in an inactive form.* Once the food comes into the stomach/intestine, the inactive zymogen gets converted into the active enzyme. The example given herewith explains the concept clearly. Pepsinogen, we learnt earlier in the sub-section 5.3.2 is the inactive form, which actually is a zymogen. HCl in the stomach activates the inactive pepsinogen to the active enzyme pepsin.

Pepsinogen (Zymogen) ⟶ Pepsin (Active Enzyme)

Now, let us learn about the different pancreatic enzymes.

A. *Trypsin*

Trypsin is secreted in the inactive form trypsinogen which is converted into the active form trypsin by the enzyme *enterokinase* secreted by the duodenal mucosa. Trypsin acts upon the native proteins, proteoses and peptones and converts them to polypeptides and peptides as indicated in Figure 5.2. It attacks the peptide linkages containing arginine or lysine residues.

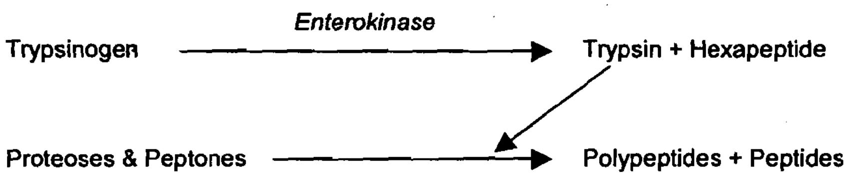

Figure 5.2: Role of trypsin

B. *Chymotrypsin*

Chymotrypsin is secreted in an inactive form 'chymotrypsinogen', which is activated by trypsin as shown in Figure 5.3. Chymotrypsin is specific for peptide bonds containing uncharged amino acid residues such as aromatic amino acids.

C. *Elastase*

The inactive *proelastase* is activated by trypsin to the active form *elastase* as can be seen in Figure 5.3. Elastase attacks peptide bonds next to the small amino acid residues such as glycine, alanine and serine and has a broader specificity than the other two enzymes.

All the three enzymes viz. trypsin, chymotrypsin and elastase are *endopeptidases* (a subclass of peptide hydrolases that hydrolyse the more centrally situated peptide bonds). You have already seen that pepsin is also an endopeptidase.

D. *Carboxypeptidase*

The inactive zymogen procarboxypeptidase is activated by trypsin as shown in Figure 5.3. The further action on the polypeptides is carried out by carboxypeptidase which attacks the carboxy terminal peptide bond, liberating single amino acids. So you realize that carboxypeptidase hydrolyses peptide bonds from the end of the peptide chain. Therefore, it is called as an *exopeptidase* (unlike trypsin, chymotrypsin and elastase). Further, since this enzyme acts on the peptide bonds of the peptide chain containing free COOH (carboxylic) group, it is specifically called *carboxypeptidase.*

The action of each of the specific enzyme discussed above is summarized in Figure 5.3.

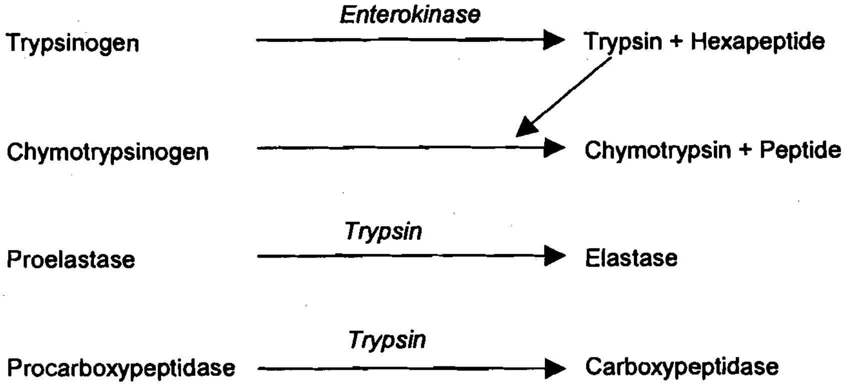

Figure 5.3: Activation of zymogens by trypsin

E. *Amylase*

The presence of pancreatic amylase brings about the breakdown of starch and glycogen and its action is similar to salivary amylase. The hydrolysis of starch and glycogen produces maltose, maltotriose and a mixture of branched oligosaccharides (α- limit dextrin), non branched oligosaccharides and some glucose.

F. *Lipase*

Pancreatic lipase specifically hydrolyses the primary ester linkages i.e. at the position 1 and 3 of triacylglycerols. The presence of bile salt helps in emulsification of fat, thereby, increasing fat digestion. 2-monoglyceride (2-monoglycerol) and fatty acids are the major end products of fat digestion and one fourth of the dietary triacylglycerol is completely broken down to glycerol and fatty acids as shown in Figure 5.4.

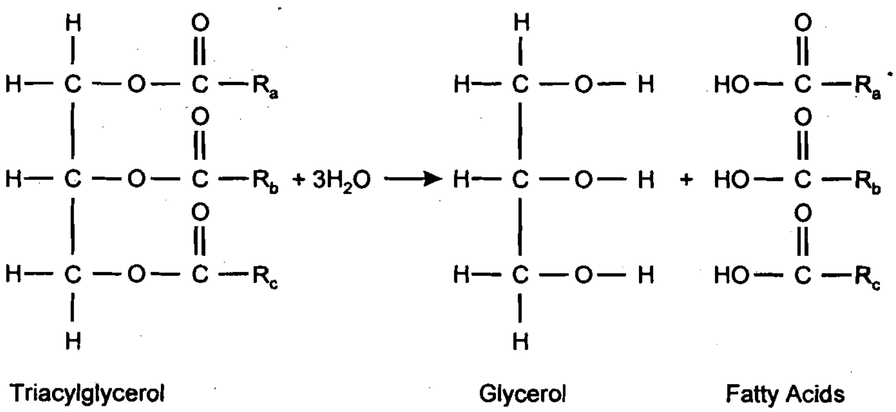

Figure 5.4: Breakdown of Triacylglycerol to glycerol and fatty acids

Cholestryl ester hydrolase acts upon cholesteryl esters to liberate free cholesterol and fattv acids. *Phospholipases* break down phospholipids.

G. *Ribonucleases, Deoxyribonucleases, Phosphodiesterases*

These enzymes are responsible for the degradation of dietary nucleic acids. *Ribonucleases* and *deoxyribonucleases* secreted by the pancreatic juice hydrolyze RNA and DNA to oligonucleotides. These are further hydrolyzed by pancreatic *phosphodiesterases* producing a mixture of 3' and 5' mononucleotides. *Nucleotidases* remove the phosphate groups hydrolytically releasing nucleosides. These are absorbed by the mucosal cells or may be further degraded to free bases before uptake.

We have so far studied about the different enzymes produced by the pancreas. How are these pancreatic secretions controlled? Let's find out. The pancreas releases its digestive juice when stimulated by *secretin*, a hormone produced in the duodenum in response to *chyme* (the complex contents of the stomach). Secretin causes the secretion of an almost protein free electrolyte solution that has a high concentration of bicarbonate. *Pancreozymin* or *cholecystokinin-pancreozymin* is a hormone released from the mucosa of the duodenum, which causes the release of an enzyme–rich juice from the pancreas.

Next, we shall look at the role of bile in digestion.

5.3.4 Role of Bile in Digestion

Bile is produced by liver and stored in gall bladder. During digestion, the gall bladder contracts and supplies bile, rapidly to the duodenum through the common bile duct.

As compared to the bile produced by liver (hepatic bile), the bile stored in gall bladder is more concentrated (since water is absorbed during the storage period in the gall bladder) and high in bile salts, cholesterol and pigments. Bile acids are cholic acid and deoxycholic acid and salt of these acids with glycine and taurine are known as *bile salts*. Bile salts have a considerable ability to lower surface tension. By this property, they prevent the coming together of the small fat droplets in the intestine and thus allow more rapid digestion of the fat. This is called the *emulsification action of bile*. Bile salts also combine with fatty acids and render them more easily absorbed. This is called *hydrotropic action of bile*. The presence of bile in the intestine is to accomplish digestion and absorption of fat and also of fat-soluble vitamins.

Finally, the partly digested food enters the intestine. Let us study about the process of digestion in the intestine.

5.3.5 Digestion in the Intestine

About 2 to 3 liters of alkaline fluid is secreted every day by the intestine and completes the digestive process. Sodium bicarbonate and sodium chloride are the main inorganic components. The organic components include enzymes such as *aminopeptidases, dipepetidases* of various specificity, specific *disaccharidases, phospholipases* etc. Let us get to know about these enzymes and about the control of these (intestinal) secretions.

Enzymes of intestinal juice

Aminopepetidase is an exopeptidase and cleaves peptide bonds next to N-terminal amino acids of polypeptides and oligopeptides (unlike carboxypeptidase which acts on peptide bond at the C (carboxy) terminal). Dipeptidase completes the digestion of dipeptides to free amino acids.

Next, let us see how the intestinal secretions are controlled.

Control of intestinal secretion

There are specific disaccharidases and oligosaccharidases i.e. α glucosidase (maltase) which removes single glucose residues from α ($1 \rightarrow 4$) linked oligosaccharides and disaccharides, starting from the non-reducing ends. *Isomaltase* (α-dextrinase) hydrolyses $1 \rightarrow 6$ bonds in α-limit dextrins. *β-galactosidase* (lactase) removes galactose from lactose (i.e. hydrolyses lactose to galactose and glucose) and *sucrase* hydrolyses sucrose to glucose and fructose.

- The intestinal juice contains *phospholipase* that attacks phospholipids to produce glycerol, fatty acids, phosphoric acid and bases such as choline.

The intestinal secretion is stimulated by enterokinase produced by jejunum, of the small intestine, which in turn is released by the entry of acid chyme from the stomach to duodenum.

In this section we studied about the process of digestion in the mouth→stomach pancreas→ intestine. We have seen that the process of digestion is achieved through the secretions (enzymes) secreted by the organs of the digestive system. Next, we shall look at the digestion of food material. But, first let us try to answer the questions given in check your progress 1. These will test your understanding on the topic covered so far.

Check Your Progress Exercise 1

1) What do you understand by the term 'digestion'? What is the major site of absorption?

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2) List the various organs involved in digestion process.

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3) What is saliva? What is its role in digestion?

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4) Describe the digestive process occuring in the stomach.

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5) Describe the composition of pancreatic juice.

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6) Explain the emulsification action of bile.

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7) List the enzymes of intestinal juice.

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5.4 DIGESTION OF FOOD MATERIALS

Digestion, you know, *involves the mixing of food, its movement through the digestive tract and chemical breakdown of the large molecules of food into smaller molecules.* Digestion, you also learnt, begins in the mouth, when we chew and swallow, and is completed in the small intestine. The chemical process varies somewhat for different kinds of food/nutrients i.e. for carbohydrates, proteins, fats etc. In this section, we shall learn about the chemical process involved during the digestion of these nutrients in the body. We shall start with the digestion of carbohydrates.

5.4.1 Digestion of Carbohydrates

In the last section we saw that the digestion of food starts in the mouth itself by the action of enzyme *salivary amylase* and the carbohydrates present in the food, particularly the starch, are broken down by the salivary amylase to starch dextrins, glucose and maltose. The presence of hydrochloric acid in the stomach stops further action of salivary amylase when the food enters the stomach.

$$\text{Starch} \xrightarrow{\textit{Salivary amylase}} \text{dextrins + glucose + maltose}$$

When the chyme enters the duodenum, the alkaline pH of the pancreatic juice helps in the digestion of starch / dextrin and glycogen by pancreatic amylase. The end products are maltose, isomaltose etc.

$$\text{Starch / dextrins} \xrightarrow{\textit{Pancreatic amylase}} \text{maltose + isomaltose + } \alpha\text{- limit dextrin}$$

The enzymes from brush border membrane of small intestine complete the digestion of various disaccharides of the diet and the product of pancreatic amylase action such as maltose, isomaltose, sucrose, lactose. The final products of carbohydrate digestion are monosaccharides i.e. glucose, fructose and galactose as shown herewith.

$$\text{Maltose} \xrightarrow{\textit{Maltase}} \text{glucose + glucose}$$

$$\text{Isomaltose} \xrightarrow{\textit{Isomaltase}} \text{glucose + glucose}$$

$$\text{Sucrose} \xrightarrow{\textit{Sucrase}} \text{fructose + glucose}$$

$$\text{Lactose} \xrightarrow{\textit{Lactase}} \text{galactose + glucose}$$

Remember, cellulose is not digested in the human GI tract due to the absence of the enzyme cellulase.

Next, we shall study about the digestion of proteins in our body.

5.4.2 Digestion of Proteins

The proteolytic enzymes secreted by gastric juice, pancreatic juice and intestinal juice cause the hydrolysis of proteins in the gastrointestinal tract. With the exception of the intestinal peptidases, all proteolytic enzymes are activated by the conversion of inactive large precursors called zymogens to functional enzymes. Recall reading about this in the last section. The enzyme pepsin acts on food proteins and converts them into proteoses and peptones.

$$\text{Food proteins} \xrightarrow{\textit{Pepsin}} \text{Proteoses and peptones (large polypeptides)}$$

The polypeptides formed in the stomach are digested in the intestine by *trypsin, chymotrypsin, elastase* and *carboxypeptidases* secreted in the pancreatic juice.

$$\text{Polypeptides} \xrightarrow{\textit{Trypsin, chymotrypsin}} \text{Peptides + amino acids}$$

$$\text{Peptides} \xrightarrow{\textit{Carboxypeptidase}} \text{Amino acids}$$

The products of these enzymes are free amino acids, dipeptides and small peptides. The residual peptides are hydrolysed in the intestinal mucosal cells by *aminopeptidases* and *dipeptidases*. Figure 5.5 graphically presents the process of protein digestion. The final breakdown products of protein digestion are single amino acids or small chains of two or three amino acids.

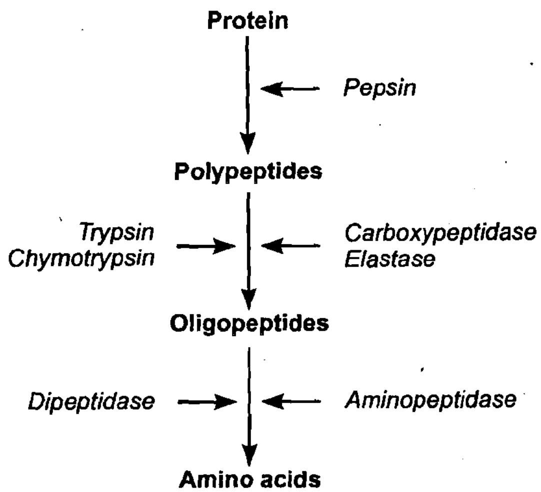

Figure 5.5: Process of protein digestion

The proteolytic enzymes have some remarkable specificity for clearing protein chain at certain amino acid residues. The specificities are summarized in Table 5.1.

Table 5.1: Specificity of some proteolytic enzymes

Enzyme	Occurrence	pH Optimum	Major site of action
Trypsin	Intestine	7.5 to 8.5	Arginyl, lysyl bonds
Chymotrypsin	Intestine	7.5 to 8.5	Aromatic amino acid bonds (Phe, Trp, Tyr)
Pepsin	Stomach	1.5 to 2.5	Wide range of specificity
Carboxypeptidase	Intestine	7.5 to 8.5	C-terminal amino acid
Aminopeptidase	Intestinal mucosa		N-terminal amino acid

After proteins, it is the turn of fats. Let us get to know about the digestion of fats in our body.

5.4.3 Digestion of Lipids

Even though lipase is present in the stomach, it remains inactive due to the acidic environment of the stomach contents. Therefore, the ingested fat is primarily digested in the small intestine.

Fat present in the food is mixed with bile and pancreatic secretion while reaching the duodenum. The bile salts emulsify the lipids before the action of pancreatic lipase.

Pancreatic lipase acts on the dietary triacylglycerols after it has been incorporated into the mixed micelle in the intestinal lumen. The lipase acts at interface between water and the triacylglycerol molecules, and its catalytic action is facilitated by the presence of *colipase* (a small protein cofactor needed by pancreatic lipase for efficient dietary lipid hydrolysis), which is also produced by the pancreas. Pancreatic lipase is specific for the fatty acid residues at positions 1 and 3 of the glyceryl moiety thus releasing 2-monoacylglycerol and two fatty acids from a triacylglycerol molecule. The final digestive products of triacylglycerol digestion are free fatty acids, glycerol and monoacylglycerols.

$$\text{Triacylglycerol} + 2H_2O \rightleftharpoons \text{2-Monoacylglycerol} + 2\ \text{Fatty acids}$$

After hydrolysis, the products diffuse from the micelle to the intestinal mucosal cell membrane. The phosphoglycerides present in the diet are digested by pancreatic *phospholipase* and cholesteryl esters are hydrolyzed to cholesterol and fatty acids through the action of cholesteryl esterase.

$$\text{Cholesterol ester} \xrightarrow{\textit{Cholesteryl esterase}} \text{Cholesterol} + \text{FFA}$$

The action of various phospholipases is presented in Figure 5.5. *Phospholipase A_1* hydrolyzes fatty acids attached to carbon 1 of the phospholipids, while *phospholipase A_2* removes the fatty acid attached to carbon 2. It is found in pancreatic juice and snake venom. In each case, the product is called *lysophospholipid. Phospholipase B* can hydrolyse both the fatty acids (at carbons 1 and 2). *Phospholipase C* attacks the ester bond in position 3 and removes phosphate + base, forming 1,2-diacylglycerol. This enzyme is present in toxins secreted by bacteria. *Phospholipase D,* found normally in plants, hydrolyses the nitrogenous base from phospholipids, forming phosphatidic acid.

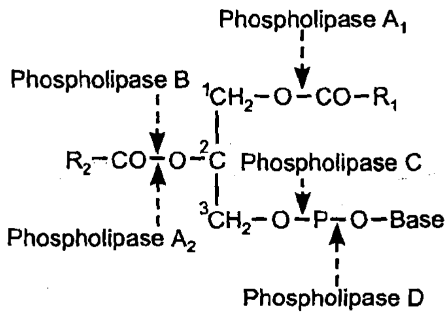

Figure 5.6: Action of various phospholipases

Finally, we shall look at the digestion of nucleic acids in our body.

5.4.4 Digestion of Nucleic Acids

Several nucleases present in the pancreatic juice like RNAase and DNAase digest various nucleic acids. These enzymes are *endonucleases* which hydrolyze internal phosphodiester bonds which are located more centrally in the nucleic acid. They form shorter length chains with 3'-hydroxyl and 5'-phosphoryl or 5'-hydroxyl and 3'-phosphoryl terminus. Some act on both the strands, whereas, others can hydrolyze only single strand of nucleic acids. *Phosphatases* present in the intestinal juice remove phosphate from hexophosphates, glycerophosphates and nucleotides derived from the food. Further, the *nucleotidases* and *nucleosidases* present in the intestinal juice hydrolyze it to the level of respective bases as shown in Figure 5.7.

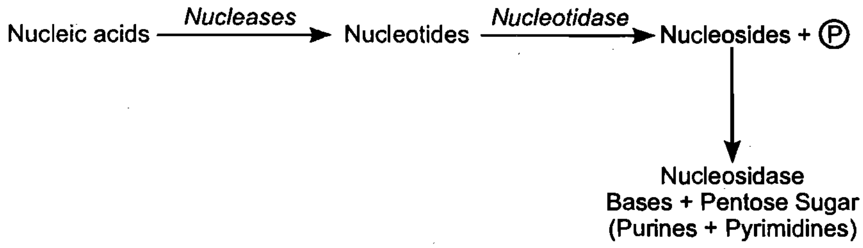

Figure 5.7: Digestion of nucleic acids

With this, we end our study on digestion. We move to the absorption process next. But before that, let us recapitulate what we have learnt till now.

Check Your Progress Exercise 2

1) Name the various enzymes involved in the digestion of carbohydrates. Enumerate the reactions catalyzed by these.

2) What are the final breakdown products of proteins? Explain giving suitable reactions involved.

3) Explain the role of lipase in lipid digestion.

4) What are 'endonucleases'? What is their site of action and end products?

5.5 ABSORPTION AND TRANSPORT

We already know that the movement of substances into or across tissues, in particular, the passage of nutrients and other substances into the walls of the gastrointestinal tract and then into the bloodstream is referred to as *absorption.*

The small intestine is the main digestive and absorptive organ. Most absorption occurs in the duodenum and jejunum (second third of the small intestine). You may have already studied the anatomy of small intestine in the Applied Physiology Course. If not, we suggest you look up Unit 6 of the Applied Physiology Course now.

Transport across the intestine may be *active* or *passive.* Active transport requires energy, whereas passive transport does not. Also, active transport may involve movement of a substance *against* a concentration gradient (that is, from a region of lower to higher concentration), while substances that are passively transported always move *with* the concentration gradient. *Facilitated diffusion* is a type of passive transport which, unlike simple diffusion, uses a *carrier.* It is therefore more rapid than simple diffusion. *Active transport* mechanisms have been identified for intestinal absorption of many substances including glucose, galactose, amino acids, calcium, iron, folic acid, ascorbic acid, thiamin and bile acids. Fructose, riboflavin and vitamin B_{12} (in combination with intrinsic factor) are among the substances absorbed by *facilitated diffusion*. Look up Unit 8 in the Applied Physiology Course to know about active and passive transport across cell-membrane. This information will help you understand the absorption of different nutrients discussed here in this unit.

We shall study the absorption of different nutrients, namely carbohydrates, proteins and fats in this section. We start with the absorption of carbohydrates.

5.5.1 Absorption of Carbohydrates

Absorption of carbohydrates is via both passive and active transport. Let us learn how.

- *Passive transport*

The end products of carbohydrate digestion are monosaccharides. They are absorbed from the jejunum into the portal blood system, through which they are transported first to the liver and then to the rest of the body. Pentoses and fructose pass across the intestinal barrier by simple passive diffusion and also by facilitated diffusion involving carrier proteins.

- *Active transport*

D-glucose and D-galactose are absorbed by an active transport mechanism. The active transport of glucose is illustrated in Figure 5.8. The transport of glucose is facilitated by a carrier protein, which has separate binding sites for glucose and sodium. Both are transported through the plasma membrane and after releasing sodium and glucose into the cytosol (liquid medium of the cytoplasm), the carrier protein return to take up fresh load. The sodium is transported down its concentration gradient and at the same time causes the carrier to transport glucose against its concentration gradient. The free energy required for this active transport is obtained from the hydrolysis of ATP linked to sodium pump which expels Na^+ from the cell.

The active transport of glucose is inhibited by *Ouabain* (a cardiac glycoside), an inhibitor of the sodium pump and by *phlorihizin,* a known inhibitor of glucose re-absorption in the kidney tubules.

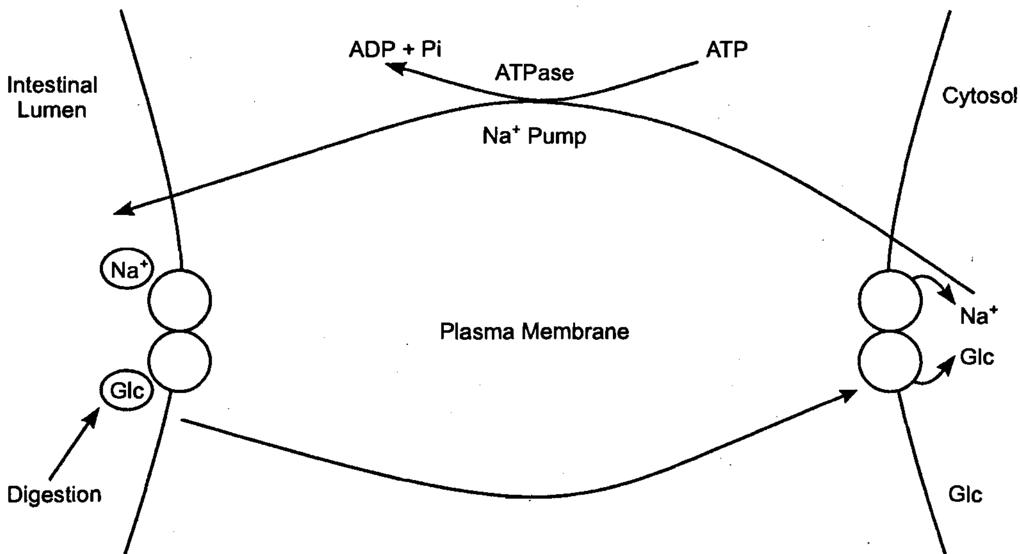

Figure 5.8: Active transport of glucose

There is also a sodium independent carrier of glucose.

5.5.2 Absorption of Proteins

In sub-section 5.3.2, we have seen how the proteolytic enzymes break the dietary proteins into amino acids or di- and tripeptides. In fact, it is in this form that the dietary proteins are absorbed. Dietary proteins are, with very few exceptions, not absorbed. Digestion of proteins and absorption of amino acids goes on throughout the small intestine. We shall look at the mechanism of absorption of amino acids and peptides next.

Absorption of amino acids and peptides

Generally, the dietary proteins are almost completely digested to their constituent amino acids and these are rapidly absorbed from the intestine into the portal blood. Some of the dipeptides are hydrolyzed by *peptidases* located in the absorptive cells so that only amino acids are released into the portal blood. D-amino acids are absorbed by simple diffusion but the L-amino acids (occurring in foods) require a carrier system in the absorption.

The mechanism by which amino acids are absorbed is conceptually identical to that of monosaccharides. The luminal plasma membrane of the absorptive cell bears at least four sodium-dependent amino acid transporters (one each for acidic, basic, neutral and aromatic amino acids), as highlighted in Table 5.2. Each system transports amino acids that are structurally similar. These transporters bind amino acids only after binding sodium. The fully loaded transporter then undergoes a conformational change that dumps sodium and the amino acid into the cytoplasm, followed by its reorientation back to the original form. Thus, absorption of amino acids is also absolutely dependent on the electrochemical gradient of sodium across the epithelium. The energy dependent carrier system also involves vitamin B_6 (pyridoxal phosphate) during the transport of amino acids.

Apart from amino acids, a substantial amount of small peptides are also absorbed by stereospecific (determined by structure of amino acid) transport systems. These small peptides are absorbed without dependence on sodium, probably by a single transport molecule. The uptake mechanisms for peptides are separate from those for amino acids.

Table 5.2: Amino acid transport systems

	Amino acid specificity	Examples of amino acid transported
1	Small neutral amino acids	Alanine, serine and threonine
2	Large neutral and aromatic amino acids	Isoleucine, leucine, valine, tyrosine, tryptophan, phenylalanine
3	Basic amino acids	Arginine, lysine, ornithine
4	Acidic amino acids	Glutamic acid, aspartic acid

We have seen that dietary proteins as such cannot be absorbed. But, absorption of intact proteins does occur only in a few circumstances. What are these circumstances? Let's find out.

Absorption of proteins in infants

In infants, permeability of the intestine appears to be greater than in later life, and some large protein molecules such as antibodies in the mother's milk and protein allergens pass by diffusion through the wall. Pinocytosis appears to account for the absorption of these large molecules in children and adults. Pinocytosis, as you may recall reading in the Applied Physiology Course, is a process by which certain cells can engulf and incorporate droplets of fluid. Look up Unit 2, sub-section 2.3.1 in the Applied Physiology Course for understanding this process.

Next, let us look at the absorption of lipids.

5.5.3 Absorption of Lipids

Lipids are absorbed by a mechanism distinctly different from what we have seen for monosaccharides and amino acids. In fact absorption of dietary triacylglycerols and medium chain triacylglycerols in the food also varies. Let us get to know this process in greater detail.

Absorption of long-chain triacylglycerols

The triacylglycerols present in the ordinary food that we eat contains long chain fatty acids (mostly 16 and 18 carbon-atom saturated and unsaturated fatty acids). *Pancreatic lipase* specifically acts upon the fatty acid residues at positions 1 and 3 of the glyceryl moiety thereby producing 2-monoacylglycerols and the released fatty acids can pass through cell membrane, and they are absorbed by diffusion into the mucosal cells of the jejunum and ileum. There is resynthesis of triacylglycerol moiety inside the mucosal cells and this reformed triacylglycerol is coated with protein, cholesterol or phospholipid to form tiny globules called *chylomicrons* as shown in Figure 5.9. Instead of being absorbed directly into capillary blood, these chylomicrons are transported first into the lymphatic vessel that penetrates into each villus. Chylomicron-rich lymph then drains into the system lymphatic system, which rapidly flows into blood. Blood-borne chylomicrons are rapidly disassembled and their constitutent lipids utilized throughout the body.

Absorption of medium-chain triacylglycerols

Medium chain triacylglycerols with fatty acids containing less than 10 to 12 carbons are absorbed intact either onto the mucosal cell villi or into the cells and are hydrolyzed to free fatty acids and glycerol by the lipase present inside the cell. The released fatty acids pass directly into the portal vein. Plasma albumin acts as a carrier for these fatty acids and delivers them to the liver as fatty acids by portal circulation.

The difference in digestion and absorption of dietary triacylglycerols and medium chain triacylglycerols is illustrated in Figure 5.9.

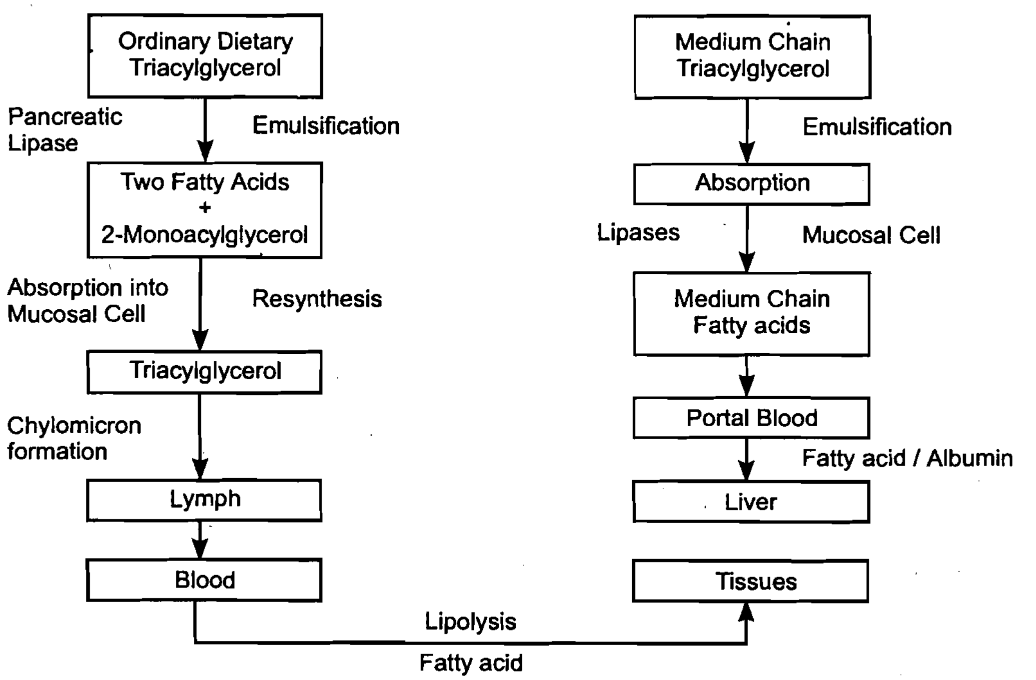

Figure 5.9: Difference in digestion and absorption of dietary triacylglycerols and medium chain triacylglycerols

Another lipid of importance that is absorbed in the small intestine is *cholesterol.* A specific transport protein has been identified that ferries cholesterol from the intestinal lumen into the enterocyte. From there, cholesterol is incorporated into chylomicrons and shuttled into blood by the mechanisms described above.

So we have looked at how the fats are absorbed in the body. Now the fats (lipids) absorbed from the diet must be transported in the blood. Blood plasma is a watery environment. We also know that lipids are insoluble in water. So how are they transported in blood? Well, fats are insoluble in water and so lipid compounds such as cholesterol, fatty acids, oil soluble vitamins and triglycerides need to be associated with proteins, forming water soluble *lipoproteins,* in order to be transported around the body.

Most lipids are transported in the blood as triacylglycerols within lipoprotein (particles containing a core of hydrophobic lipids surrounded by a shell of proteins, phospholipids and cholesterol). Four major groups of lipoproteins help in transport of lipids. These include:

1. *Chylomicrons*-function is to carry dietary triacylglycerols
2. *Very low density lipoprotein (VLDL)*-function is to carry endogenously made triacylglycerols
3. *Low density lipoprotein (LDL)*-function is to carry cholesterol and cholesterol esters, and
4. *High density lipoprotein (HDL)*-functions in reverse cholesterol transport and exchange of apoproteins.

We shall learn more about lipoproteins later in Unit 7 under lipoprotein metabolism. With this, we come to an end of our study of digestion, absorption and transport of carbohydrates, lipid and proteins.

Check Your Progress Exercise 3

1) List the various transport mechanisms involved in the absorption of various nutrients in the intestine, giving suitable examples.

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2) How are carbohydrates absorbed in our body?

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3) Explain the active transport of glucose.

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4) Explain the process of absorption of amino acids and peptides.

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5) Bring out the major points of difference in the digestion and absorption of dietary triacylglycerols and medium chain triacylglycerols.

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6) How are lipids transported in blood? List the four major groups of lipoproteins involved in lipid transport.

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5.6 LET US SUM UP

In this unit we studied about the digestion, absorption and transport of carbohydrates, fats and proteins in our body. The salient features discussed include:

1. The digestive system takes in food, digests it to the end products, which are absorbable into the system. The non-absorbable products are eliminated.
2. The ingested food is broken down into end products through mechanical, chemical and enzymatic digestion.
3. Digestion involves the participation of mouth, esophagus, stomach, intestine, liver, pancreas and gall bladder.
4. Digestion also involves the participation of a number of enzymes viz., amylase, pepsin, trypsin, chymotrypsin, endopeptidases, aminopeptidases, carboxypeptidases, nucleases and lipases, which break down the dietary carbohydrates, proteins and lipids into simple units.
5. Control of pancreatic, liver and intestinal secretion is by hormones.
6. Most of the above enzymes are secreted in the form of pro-enzymes and get converted into active form just before their action.
7. The end products are absorbed into the system through various transport mechanisms such as active, passive mechanism etc.

5.7 GLOSSARY

Absorption : taking in the molecules from the GI tract.

Active transport : using carriers, energy (ATP) and enzymes of cell to cause a substance to cross a membrane.

Bile : a clear yellow or orange fluid produced by the liver.

Brush border : a specialization of the free surface of a cell, consisting of minute cylindrical processes (microvilli) that greatly increase the surface area.

Chyme : the thick semi-fluid mixture of partially digested foods and digestive juices found in the stomach and small intestine.

Dextrins : polysaccharides containing fewer simple sugar units than starches.

Digestion : breaking of foods using chemical or mechanical means to convert foods into chemical compounds, which could be absorbed.

Facilitated diffusion : a type of passive transport that uses a carrier.

Micelle : a submicroscopic aggregation of molecules, as a droplet in a colloidal system. Micelles are essentially small aggregates of mixed lipids and bile salts suspended within the ingesta.

Pinocytosis : the ingestion of dissolved materials by endocytosis. The cytoplasmic membrane invaginates and pinches off placing small droplets of fluid in a pinocytic vesicle. The liquid contents of the vesicle are then slowly transferred to the cytosol.

Serum lipoproteins : spherical or ellipsoidal particles containing proteins, cholesterol esters and triacylglycerols, encased within a monolayer of phospholipids and cholesterol.

Zymogen : an inactive form of an enzyme; becomes active prior to its action.

5.8 ANSWERS TO CHECK YOUR PROGRESS EXERCISES

Check Your Progress Exercise 1

1). The process through which the major nutrients namely carbohydrates, proteins and lipids are converted to simple sugars, amino acids, fatty acids and glycerol respectively, while passing from mouth to small intestine, is referred to as digestion. Microvilli of the small intestine is the major site of absorption.

2) The various organs involved in the digestion process are:
   - Alimentary tract which includes mouth, pharynx, esophagus stomach, small intestine, large intestine, appendix, rectum and anal canal, and
   - Accessory organs which include tongue, teeth, salivary glands, liver, gall bladder and pancreas.

3) Saliva is the colourless viscous fluid. It helps in swallowing the food by lubricating the food and the neutral pH of saliva prevents the decalcification of teeth and keeps the mouth clean. In the mouth, is also present the salivary amylase. The presence of salivary amylase starts the starch digestion.

4) The digestive process occurring in the stomach is discussed as:
   The stomach secretes gastric juice. The major components of gastric juice are hydrochloric acid and the enzyme pepsin which is secreted in an inactive form called pepsinogen. Hydrochloric acid (pH 1.2 – 1.5) activates the inactive pepsinogen to the active form pepsin. Hydrochloric acid denatures the food proteins for easy digestion. The pepsin produced in an active proteolytic enzyme that activates the remainder of the pepsinogen molecule by proteolytically converting them to pepsin. Digestion of protein is initiated in the stomach by pepsin. Pepsin acts upon food proteins and converts them to proteoses and peptones.

   In infants, the presence of another enzyme called rennin helps in digestion of casein to paracasein which is then acted upon by pepsin.

5) Pancreatic juice is alkaline in nature (pH about 8.0) and contains both organic and inorganic substances. The enzyme components are trypsin, chymotrypsin, elastase and carboxypeptidase. The other enzymes are amylase, lipase, cholesteryl ester hydrolase and phospholipases. Sodium, chloride and bicarbonate are the major inorganic constituents.

6) Bile salts have a considerable ability to lower surface tension. By this property, they prevent the coming together of the small fat droplets in the intestine and thus allow more rapid digestion of the fat. This is called the emulsification action of bile.

7). The enzymes of intestinal juice are aminopepetidase and dipeptidase.

Check Your Progress Exercise 2

1) Salivary amylase, pancreatic amylase, maltase, isomaltase, sucrase and lactase are the enzymes involved in the digestion of carbohydrates. The reactions catalyzed by these are:

Starch —(Salivary amylase)→ dextrins + glucose + maltose

Starch/dextrins —(Pancreatic amylase)→ maltose + isomaltose + α- limit dextrin

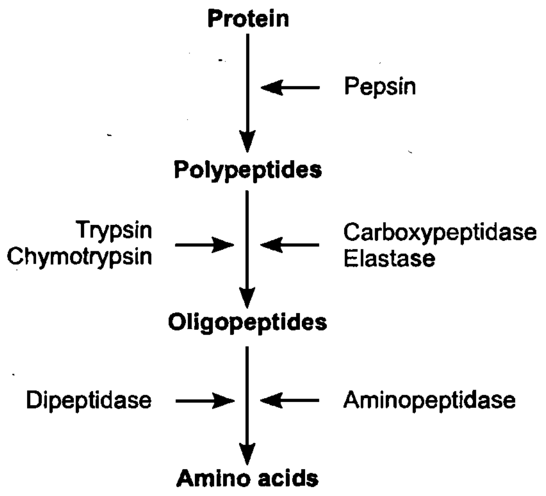
Maltose —(Maltase)→ glucose + glucose

Isomaltose —(Isomaltase)→ glucose + glucose

Sucrose —(Sucrase)→ fructose + glucose

Lactose —(Lactase)→ galactose + glucose

2) The final breakdown products of protein digestion are single amino acids or small chains of two or three amino acids.



3) Pancreatic lipase acts on the dietary triacylglycerol after it has been incorporated into the mixed micelle in the intestinal lumen. The lipase acts at interface between water and the triacylglycerol molecules, and its catalytic action is facilitated by the presence of colipase. Pancreatic lipase is specific for the fatty acid residues at positions 1 and 3 of the glyceryl moiety thus releasing 2-monoacylglycerol and two fatty acids from the triacylglycerol molecule. The final digestive products of triacylglycerol digestion are free fatty acids, glycerol and monoacylglycerols.

4) Endonucleases are nucleases present in the pancreatic juice like RNAase and DNAase. These hydrolyze internal phosphodiester bonds which are located more centrally in the nucleic acid. Phosphatases present in the intestinal juice remove phosphate from hexophosphates, glycerophosphates and nucleotides derived from the food. Further, the nucleotidases and nucleosidases present in the intestinal juice hydrolyze it.

Check Your Progress Exercise 3

1) The various transport mechanisms involved in the absorption of various nutrients are active transport (glucose and galactose), passive transport (pentose and fructose) and facilitated diffusion (fructose and riboflavin).

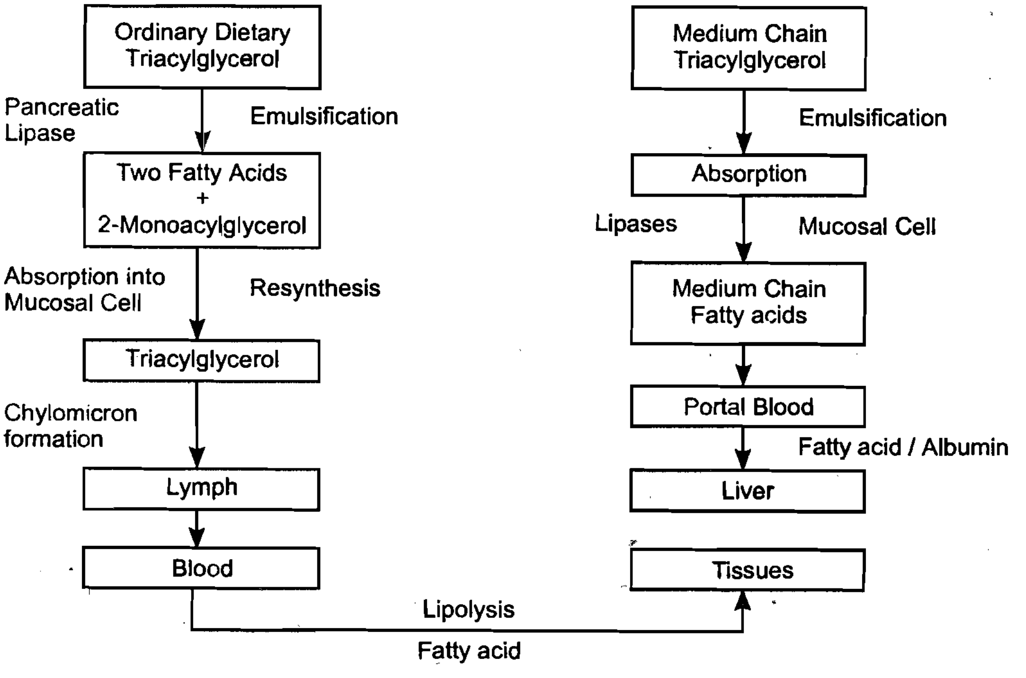
2) Carbohydrates are absorbed in our body via both active and passive transport.

3) The transport of glucose is facilitated by a carrier protein, which has separate binding sites for glucose and sodium. Both are transported through the plasma membrane and after releasing sodium and glucose into the cytosol (liquid medium of the cytoplasm), the carrier protein returns to take up fresh load. The sodium is transported down its concentration gradient and at the same time causes the carrier to transport glucose against its concentration gradient. The free energy required for this active transport is obtained from the hydrolysis of ATP linked to sodium pump which expels Na^+ from the cell.

4) The luminal plasma membrane of the absorptive cell bears at least four sodium-dependent amino acid transporters (one each for acidic, basic, neutral and amino acids). Each system transports amino acids that are structurally similar. These transporters bind amino acids only after binding sodium. The fully loaded transporter then undergoes a conformational change that dumps sodium and the amino acid into the cytoplasm, followed by its reorientation back to the original form. Thus, absorption of amino acids is also absolutely dependent on the electrochemical gradient of sodium across the epithelium. The energy dependent carrier system also involves vitamin B_6 (pyridoxal phosphate) during the transport of aminoacids.

   Apart from amino acids, a substantial amount of small peptides are also absorbed by stereospecific (determined by structure of amino acid) transport systems. These small peptides are absorbed without dependence on sodium, probably by a single transport molecule.

5) The major points of difference in the digestion and absorption of dietary triacylglycerols and MCTs can be depicted as:



6) Most lipids are transported in the blood as triacylglycerols within lipoprotein. Four major groups of lipoproteins help in transport of lipids. These include chylomicrons, very low density lipoprotein, low density lipoprotein and high density lipoprotein.