chymotrypsin, which attack the more internal parts of the protein, speeds up the process tremendously.

DIGESTION OF LIPID

Lipids

Although the American Heart Association recommends a low-fat diet, the amount of lipids (fats) ingested daily varies tremendously among American adults, ranging from 30 g to 150 g or more. The small intestine is essentially the sole site of lipid digestion because the pancreas is the only significant source of fat-digesting enzymes, or **lipases** (Figure 23.33). Neutral fats (triglycerides or triacylglycerols) are the most abundant fats in the diet.

Because triglycerides and their breakdown products are insoluble in water, fats need special "pretreatment" with bile salts to be digested and absorbed in the watery environment of the small intestine. In aqueous solutions, triglycerides aggregate to form large fat globules, and only the triglyceride molecules at the surfaces of such fatty masses are accessible to the water-soluble lipase enzymes. However, this problem is quickly resolved because as the fat globules enter the duodenum, they are coated with detergent-like bile salts (Figure 23.35). Bile salts have both nonpolar and polar regions. Their nonpolar (hydrophobic) parts cling to the fat molecules, and their polar (ionized hydrophilic) parts allow them to repel each other and to interact with water. As a result, fatty droplets are pulled off the large fat globules, and a stable *emulsion*—an aqueous suspension of fatty droplets, each about 1 μm in diameter—is formed. The process of emulsification does *not* break chemical bonds. It just reduces the attraction between fat molecules so that they can be more widely dispersed. This process vastly increases the number of triglyceride molecules exposed to the pancreatic lipases. Without bile, lipids would be incompletely digested in the time food is in the small intestine.

The pancreatic lipases catalyze the breakdown of fats by cleaving off two of the fatty acid chains, thus yielding free **fatty acids** and **monoglycerides** (glycerol with one fatty acid chain attached). Fat-soluble vitamins that ride with fats require no digestion.

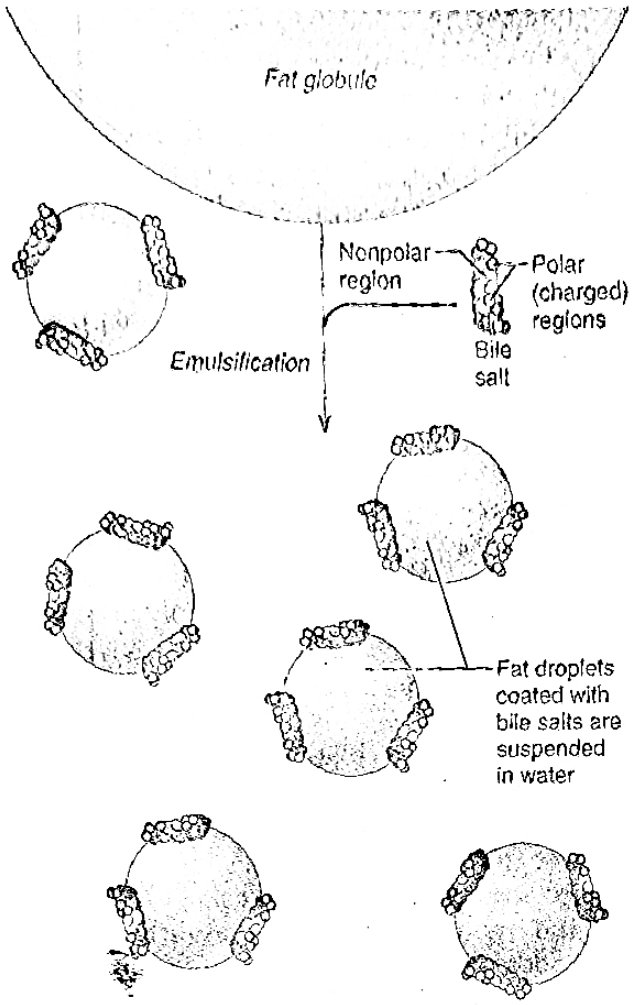

FIGURE 23.35 **Role of bile salts in fat emulsification.** As large aggregates of fats enter the small intestine, bile salts cling via their nonpolar parts to the fat molecules (triglycerides). Their polar parts, facing the aqueous phase, interact with water and repel each other, causing the fatty globule to be physically broken up into smaller fat droplets.

brush border enzymes (**nucleosidases** and **phosphatases**), which release their free bases, pentose sugars, and phosphate ions (see Figure 23.33).

Absorption

Up to 10 L of food, drink, and GI secretions enter the alimentary canal daily, but only 1 L or less reaches the large intestine. Virtually all of the foodstuffs, 80% of the electrolytes, and most of the water are absorbed in the small intestine. Although absorption occurs all along the length of the small intestine, most of it is completed by the time chyme reaches the ileum. Hence, the major absorptive role of the ileum is to reclaim bile salts to be recycled back to the liver for re-secretion. At the end of the ileum, all that remains is some water, indigestible food materials (largely plant fibers such as cellulose), and millions of bacteria. This debris is passed on to the large intestine.

Most nutrients are absorbed through the mucosa of the intestinal villi by *active transport* processes driven directly or indirectly (secondarily) by metabolic energy (ATP). They then enter the capillary blood in the villus to be transported in the hepatic portal vein to the liver. The exception is some of the lipid digestion products, which are absorbed passively by diffusion and then enter the lacteal in the villus to be carried to the blood via lymphatic fluid. Because the epithelial cells of the intestinal mucosa are joined at their luminal surfaces by tight junctions, substances cannot move *between* the cells. Consequently, materials must pass *through* the epithelial cells and into the interstitial fluid abutting their basal membranes (via *transepithelial transport*) if they are to enter the blood capillaries. Absorption of each nutrient class is described next.

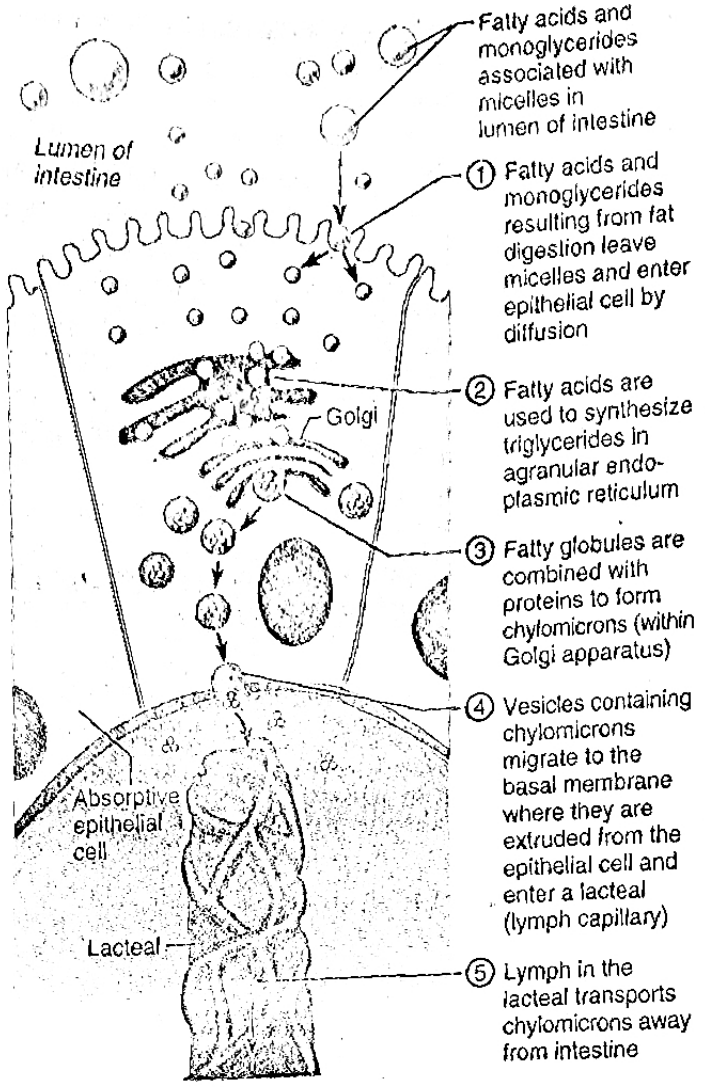

FIGURE 23.36 **Fatty acid absorption.** Digestion products of fat breakdown, lecithin, and cholesterol associate with bile salts to form micelles, which serve to "ferry" them to the intestinal mucosa. They then dissociate and enter the mucosal cells by diffusion. In the mucosal epithelial cells, they are recombined to lipids and packaged with other lipoid substances and protein to form chylomicrons. The chylomicrons are extruded from the epithelial cells by exocytosis and enter the lacteal for distribution in the lymph. Free fatty acids and monoglycerides enter the capillary bed.

usually disappear as the mucosa matures. This mechanism may also provide a route for IgA antibodies present in breast milk to reach an infant's bloodstream. These antibodies confer some passive immunity on the infant (temporary protection against antigens to which the mother has been sensitized).

Absorption of Lipids

Lipids

Just as bile salts accelerate lipid digestion, they are also essential for the absorption of its end products. As the water-insoluble products of fat digestion—

the monoglycerides and free fatty acids—are liberated by lipase activity, they quickly become associated with bile salts and *lecithin* (a phospholipid found in bile) to form micelles. **Micelles** (mi-selz′) are collections of fatty elements clustered together with bile salts in such a way that the polar (hydrophilic) ends of the molecules face the water and the nonpolar portions form the core. Also nestled in the hydrophobic core are cholesterol molecules and fat-soluble vitamins. Although micelles are similar to emulsion droplets, they are much smaller "vehicles" and easily diffuse between microvilli to come into close contact with the mucosal cell surface (Figure 23.36). The various lipid substances then leave the micelles and move through the lipid phase of the plasma membrane by simple diffusion. Without the micelles, the lipids simply float on the surface of the chyme (like oil on water), inaccessible to the absorptive surfaces of the epithelial cells. Generally, fat absorption is completed in the ileum, but in the absence of bile (as might occur when a gallstone blocks the cystic duct) it happens so slowly that most of the fat passes into the large intestine and is lost in feces.

Once inside the epithelial cells, the free fatty acids and monoglycerides are resynthesized into triglycerides. The triglycerides are then combined with phospholipids and cholesterol, and coated with a "skin" of proteins to form water-soluble lipoprotein droplets called **chylomicrons** (ki″lō-mi′kronz). These are processed by the Golgi apparatus for extrusion from the cell. This series of events is quite different from the absorption of amino acids and simple sugars, which pass through the epithelial cells unchanged.

Although a few free fatty acids enter the capillary blood, the milky-white chylomicrons are too large to pass through the basement membranes of the blood capillaries and instead enter the more permeable lacteals. Thus, most fat enters the lymphatic stream and is eventually emptied into the venous blood in the neck region via the thoracic duct, which drains the digestive viscera. While in the bloodstream, the triglycerides of the chylomicrons are hydrolyzed to free fatty acids and glycerol by **lipoprotein lipase**, an enzyme associated with the capillary endothelium. The fatty acids and glycerol can then pass through the capillary walls to be used by tissue cells for energy or stored as fats in adipose tissue. The residual chylomicron material is combined with proteins by the liver cells, and these "new" lipoproteins are used to transport cholesterol in the blood.