INTRODUCTION

Though the liver develops, embryologically, as an outgrowth from the wall of the gut, by the time it attains structural and functional maturity, it carries out multitudes of functions some of which are not necessarily connected with digestive processes. However, majority of its functions are, one way or other, correlated with digestive or metabolic activities, not because of its ontogenic relation with the gut but more because of its peculiar pattern of blood supply by which the liver has established an intimate association with the alimentary canal. The blood collected from the digestive tract is routed through the anastamosing sinusoids in the liver. Ability of liver to perform myriads of functions is to a certain extent due to the ingenuity of circulatory arrangements in the liver. For that matter, the circulation in the liver is quite unique where both the arterial and venous blood get mixed up. The portal vein carrying venous blood from the alimentary canal and spleen, together with branches of hepatic artery enter the liver at the porta hepatis and thereafter divide and run through connective tissue septa of the lobules as the interlobular vessels. These vessels eventually penetrate lobules through fine branches and they ultimately become confluent with the sinusoids. The sinusoids in turn empty into the central vein, which runs through lobules and ultimately merges into the hepatic vein. Thus, the vertebrate liver, through the course of evolution has acquired marvelous structural features whereby every hepatic cell is exposed to the circulating blood. The flow of blood through the liver is controlled by vasoconstrictor nerve fibers. Thus regulated blood flow through the sinusoids helps the liver cells to absorb materials from the blood, to remove substances from that are harmful to the body, or to add into the blood the materials formed in the liver. The major share of supply of blood to the liver is from the portal vessels. Since the degraded food stuffs from the gastro-intestinal tract are carried to the liver by the portal circulation, further metabolism of these metabolites to a greater extent, takes place in the liver. This is the reason why liver occupies a central place in the metabolism of all food stuffs.

Different types of foods are consumed by different groups of birds and these differences can be easily correlated with the feeding adaptations, depicted by each group. The feeding adaptations, impose restrictions to the diet of the birds. Thus some are exclusively carnivorous (carrion feeders), some are insectivorous while others are either frugivores or graminivores. Each of these specializations to specific type of ~~the~~ diet need not necessarily be confined to any one order or the other of the birds. Accordingly, examples of insectivores can be found in Ciconiformes, Apodiformes, Coraciformes and Passeriformes. However, almost all birds belonging to Psittaciformes are frugivores, those of Falconiformes are carnivores and those grouped under Columbiformes are graminivores. In other words individual species have independently developed adaptations to a particular type of food according to the niche they chanced to occupy. Adaptive radiations are found to be more wide spread in larger orders like Passeriformes than in smaller ones, represented by only few species, like Psittaciformes. Though most of the avian species have developed adaptations for one type of food or the other, in comparatively recent times many have become despecialized as far as the food is concerned, in spite of the fact that their external and internal anatomy still tend to show adaptations, mostly to one type of food. For example, bird like Koel takes both fruits and insects, though the beak and gizzard are adapted generally for fruits only. Many of the Passerines have, similarly, become despecialized and have become omnivores. The omnivorous habit presents the birds with added advantages in occupying any type of habitat and thus can be omnidistributed too. Not surprisingly, birds like crows, mynas and sparrows can survive any where because of their despecialization in feeding habits. With respect to food, paradoxically, several species of birds survive due to extreme adaptations, while several others survive because they disregard their basic adaptations and become omnivorous.

The liver being intimately associated with the metabolism of food stuffs, the adaptation of birds to one type of food or lack of it should necessarily be reflected in the metabolic machinery of the organ. Perhaps even the anatomical variations like size and structure of liver should be expected, if parallel is to be drawn from the studies on mammalian livers. Magnan (1910a) noted that the liver size (liver weight as percentage of body weight) is much larger in insectivore birds followed by carnivore ones. Similar relationship of liver weight and diet has been noted in birds that are presently studied (Chapter 1). Not only the gross morphology but also the microanatomy of the organ has been found to differ in different species of birds and in Chapter 1 an attempt is made to record and establish possible parallelism in the microanatomical features of liver within the group of birds having similar diet.

Among the metabolic adaptations shown by the liver with respect to diet, those concerned with the homeostasis of circulating metabolites have considerable importance. Excess of metabolites that are absorbed by the gastro-intestinal tract are removed and stored by the liver to maintain steady levels of the metabolites in the blood. If their levels fall in the blood, the liver releases the stored reserves of the required metabolites to maintain their standard specific level. Thus, homeostasis of circulating metabolites is possible because of the capacity of liver to store large amount of carbohydrate and lipids and also because of the machinery that readily converts carbohydrate into lipids, and lipids and protein into carbohydrate. Excess of metabolites derived from food are normally stored as fat and to a certain extent as glycogen. The lipid synthesis and storage mechanisms are adaptive in nature with respect to the type of diet. Histochemical demonstration of various types of lipids in the livers of representatives of all four groups of birds (grouping done on the basis of diet) were carried out to note the adaptive features of liver with respect to the food types. The livers of omnivores not only ~~present~~

present regional variation in the distribution of neutral fat in the lobules, but also show specialized cells of reticuloendothelial system that are capable of storing fat (Chapter 2). In carnivores, insectivores, frugivores and graminivores the distribution of neutral fat is uniform in the hepatic lobules in which case it is reasonable to believe that all hepatic parenchymal cells constituting the lobular unit exhibit equal capacity to synthesize and store neutral fat. However, in omnivores only the hepatic cells of certain areas of lobule show higher capacity of lipid synthesis and storage, and the remaining cells are probably not endowed with ~~such~~ enzyme ~~machinery which influences~~ the synthesis of fat and/or have lesser capacity to store it. This may probably be due to the fact that these cells (having no lipids) are equipped with machinery to deal with the nitrogenous compounds. Thus the liver of omnivore birds, having regional specialization for metabolizing various nutrients, could easily cope up with any type of metabolites brought to it ~~by blood from the gastro-intestinal~~ tract.

The metabolic adaptations of the liver with respect to food, would involve adaptive changes in the activities of enzyme complex in the parenchymal cells. To understand such adaptive features, studies on distribution ~~and~~

and localization of certain enzymes were deemed worthwhile.

In Chapter 3 observations from histochemical studies on some enzymes concerned with lipid metabolism namely, lipase, esterase and β-hydroxybutyrate dehydrogenase are recorded. Though variations in intensity of reactions of lipase were evident in the livers of individual species within and between the groups, the enzyme was found uniformly distributed in all parts of liver lobules. As far as lipase is concerned the metabolic adaptation is perhaps in its concentration rather than in its distribution in various zones of lobules. The esterase presented a vivid differences in pattern of its distribution in liver lobules. The pattern of distribution was specific to each group except in omnivores. However, the livers of omnivores had no particular pattern of distribution characteristic of the group. This variation within the group could be explained in terms of adaptive despecialization of food habits exhibited by the omnivore birds.

β-hydroxybutyrate dehydrogenase, an NAD linked mitochondrial enzyme, was found to have a uniform distribution in the hepatic lobules of birds of all groups except that of the omnivores. In the livers of omnivores the BDH activity was found more localized around the portal areas, A fact that could be construed out of these observations is that the parenchymal cells in these areas of livers of omnivores ~~is that the parenchymal cells in these areas of livers of omnivores~~ have more mitochondria. This preferential high content of mitochondria in the cells around the portal areas, however, is not a characteristic feature of the livers of omnivores only. Therefore, it could be that the mitochondria in the cells of the liver of omnivores contain a larger quantity of BDH than in those of other groups. BDH invariably converts acetoacetic acid to D-β-hydroxybutyrate which leaves the liver to be metabolized in the extra hepatic tissues. Perhaps ketone bodies are formed more in omnivores than in other groups.

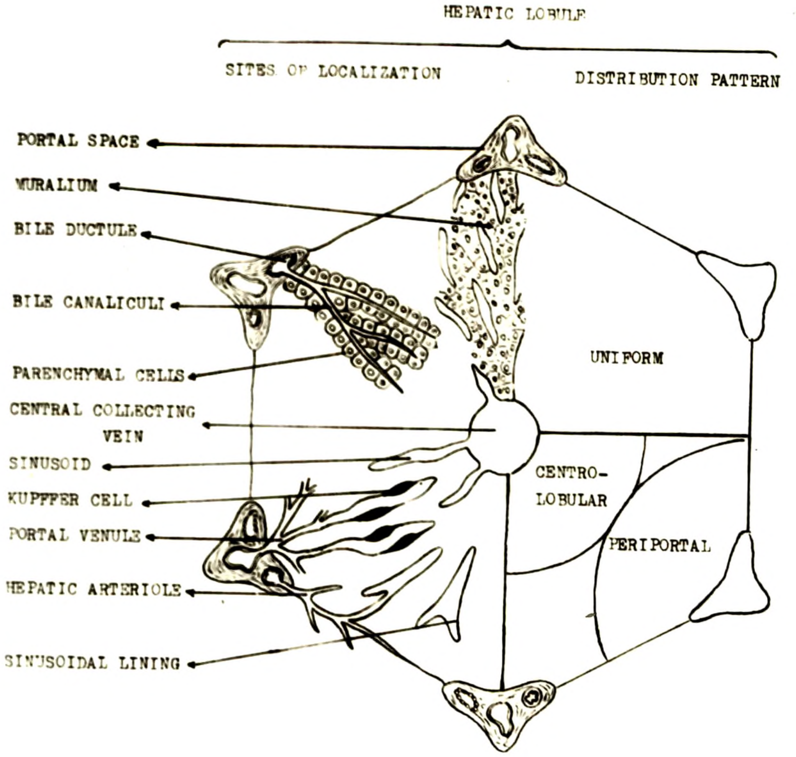
Apart from the metabolic activities, the liver performs a large number of other functions connected with secretion, excretion, phagocytosis, detoxification, storage and synthesis of vitamins, catabolism of humoral and hormonal substances and many others which are not basically integrated with the metabolism of nutrient substances. All these activities require an expenditure of energy. The liver, thus, has its own machinery to trap energy from the metabolites through anaerobic and aerobic reactions. The operation of anaerobic and aerobic pathways of metabolism could be easily envisaged from the intensity of activity of certain enzymes like α-GPDH, LDH, SDH, and MDH. Distribution and localization of these enzymes were studied using histochemical techniques in the livers of representatives of all the four groups of birds presently used for the investigation (Chapter 4). All these dehydrogenases are NAD dependant. However, SDH is found only in mitochondria, LDH is extramitochondrial while α-GPDH and MDH are both mitochondrial as well as extramitochondrial in localizations. This can be clearly seen in the histochemical preparations, as SDH is found densely localized around portal areas where number of mitochondria are more, LDH exhibited a uniform distribution. The other two dehydrogenases while enjoying a dense distribution all over hepatic lobules, also had slightly higher periportal accumulation in the livers of many birds. As far as these enzymes are concerned, except such variations in the localizations, there were no other adaptive characteristics in the livers which could be correlated with the varying food preferences of the birds. Perhaps there may be quantitative variations which can not be precisely seen in histochemical preparations.

Among the metabolic activities taking place in the liver, phosphorylation and dephosphorylation reactions occupy key roles. Many metabolites are phosphorylated or dephosphorylated while they are transported across the plasma membrane or while they are actively degraded to release energy. Alkaline and acid phosphatases are group of enzymes that are credited with the responsibility of many of such phosphorylation and dephosphorylation reactions. The histochemical studies on alkaline and acid phosphatases in the avian livers (Chapter 5) revealed interesting variations in the distribution, localizations and intensity of their reactivity which could be correlated with the dietary preference of the birds. In carnivores, insectivores and omnivores alkaline phosphatase was found heavily concentrated in portal areas where the enzyme may be participating in the transport of materials across the cell membranes. In graminivores the enzyme was generally distributed uniformly all over the lobules, while in carnivores, insectivores and omnivores the enzyme was also found in peribiliary region denoting the enzyme's participation in bile secretion in these birds. It is especially interesting to note that birds of the first three groups (carnivores, insectivores and omnivores) have gall bladder while in the birds belonging to graminivore group it is absent. Acid Pase was generally found in Kupffer cells where the enzyme could participate in phagocytosis. In carnivorous birds, like vultures and kites, the Kupffer cells showed a high activity of Acid Pase. This may be to deal with bacteria, other microbes and toxins taken along with the decaying flesh. In addition The livers of graminivores contained higher concentration of Acid Pase in the parenchymal cells ~~too~~. Such a high incidence of acid phosphatase activity in the parenchymal cells could be correlated with the metabolic reactions especially with that of triglycerides and phospholipids.

Like alkaline phosphatase, ATPase was found also to have a uniform distribution pattern but it was in a higher concentration around the bile canaliculi of all the birds studied (Chapter 6). From this, one can surmise that ATPase in the liver of birds is well concerned with the production and secretion of bile. Since there was no apparent difference in the patterns of distribution of ATPase in birds with different dietary preferences, one is lead to believe that dietary differences have not influenced the localization or distribution of ATPase in their hepatic lobules.

In Chapter 7, histochemical studies on the cholinesterases are recorded. These enzymes are known to maintain ionic concentrations of the cell membrane, and increases its permeability by action on proteins or lipoproteins components of the active membrane. BuChE is concerned with fat metabolism by releasing choline or choline like substance from their bound state. The pattern of distribution of cholinesterase was typical and characteristic of each group of birds. The carnivorous birds (kite and vulture) showed cholinesterases in the lining of hepatic sinusoids as well as blood vessels and that too only in the region around the portal areas. In insectivores and graminivores the sinusoidal lining only exhibited these enzyme activity and their localization was uniform all over their liver lobules. The omnivore birds presented varied patterns of cholinesterase distribution in their livers. Some of the omnivores studied exhibited periportal localization of both the cholinesterases (specific and non-specific) while in some others that was uniform all over the hepatic lobules. In general, almost all the omnivores showed activities of these enzymes localized in the sinusoidal lining only. However, some of them did exhibit the enzymes in parenchymal cells also. Like in the omnivores and insectivores the cholinesterase activity in the livers of frugivores and graminivores was confined to the sinusoidal lining.

The feeding adaptations of birds are usually seen in the structures of their beak, claws and gizzard and also in many other physiological processes like digestive activities. Adaptations characteristic to particular diets are exhibited by carnivores, frugivores and graminivores. Insectivores, physiologically, should resemble carnivores, but since the food is not so hard in its consistency there is no requirement of hard beak or gizzard with heavy musculature. The distribution of enzymes within the hepatic lobules, which could be considered as a measure of physiological adaptations, showed that the enzyme patterns in the livers of insectivores are more or less like that found in carnivores. The omnivore group comprises of birds that have secondarily taken to eating mixed type of foods, but their physiological as well as morphological adaptations remain more or less same as that which their ancestral birds had prior to becoming omnivores. In general, the present studies were confined to four groups of birds viz., carnivores (Group I), insectivores (Group II), omnivores (Group III) and graminivores(Group IV). However, there is another group of birds (according to their food and feeding habit) which do not fall into any of these categories. This group comprises of nectar feeders, the representative bird studied is the sunbird. Histochemical observations on the distribution and localizations of all the enzymes and metabolites that were studied in the livers of other birds, were also made on the liver of the sunbird. The observations and inferences drawn from these studies are recorded in Chapter 8. From the distribution of various enzymes it could be reasoned ~~out~~ that nectar feeder shows basically the same adaptational features as ~~that are~~ seen in the insectivores. In other words sunbird is primarily adapted to insect food and has secondarily got adapted to nectar feeding. Not surprisingly, the sunbird still consumes insects, grubs and spiders though its main food is nectar.


HEPATIC LOBULE
SITES OF LOCALIZATION
DISTRIBUTION PATTERN
PORTAL SPACE
MURALIUM
BILE DUCTULE
BILE CANALICULI
PARENCHYMAL CELLS
CENTRAL COLLECTING VEIN
SINUSOID
KUPFFER CELL
PORTAL VENULE
HEPATIC ARTERIOLE
SINUSOIDAL LINING
UNIFORM
CENTRO-LOBULAR
PERIPORTAL